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Hormones and Secondary Sex Characters

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The American Genetic Association

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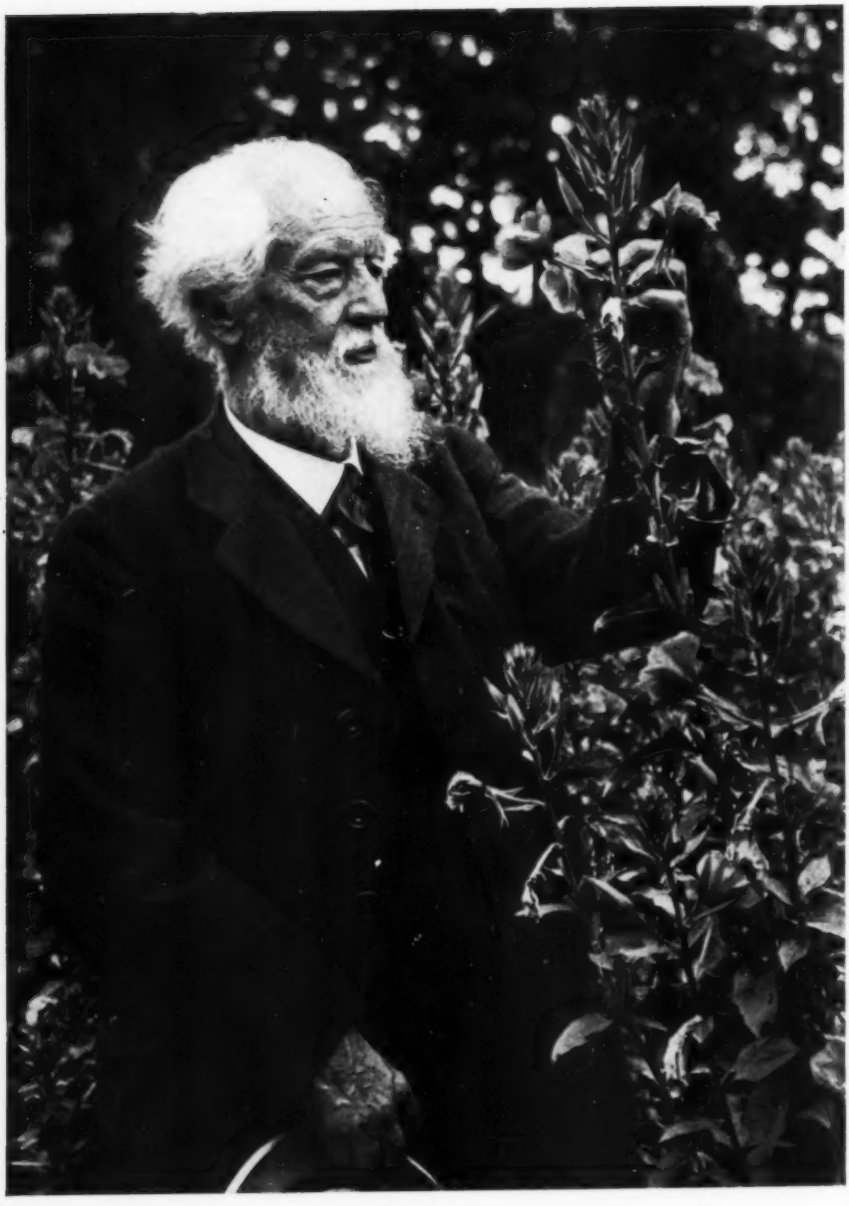

Hugo de Vries.

HUGO DE VRIES

1848—1935

ON MAY 21st, 1935, Hugo de Vries, one of the most significant figures in the history of biological thought, died after a brief illness. For the last seventeen years he and his wife had occupied a delightful estate on the outskirts of the little village of Lunteren, in central Holland. There he had built a laboratory, and developed an experimental garden; and there to the very end he had continued the genetical investigations begun many years before at the University of Amsterdam. Thus, death found him, though full of years, still in the midst of his labors.

Hugo de Vries was born in Haarlem, February 16, 1848. His father was Secretary of the Province of North-Holland, and later Minister of Justice of the Netherlands. His mother was the daughter of Professor Reuvens of the University of Leiden. From boyhood he seems to have been interested in botany; a family tradition has it that when, as a small boy, he was offered the choice between a piece of cake and a flower, he chose the flower![1] At the age of 13, he won a prize for the best collection of 100 pressed plants from the vicinity of Haarlem. At 21, he won a gold medal offered by the University of Groningen for a prize essay, his paper being entitled "Ueber die Wirkung der Wärme auf der Wurzeln der Pflanzen."

From 1866 to 1870 de Vries studied at Leiden. The controversy over Darwinism was still raging at this time, and in his doctoral dissertation, written in 1870, he made it evident that he was in sympathy with the Darwinian point of view—in opposition, it is said, to the attitude of some of his teachers.[1]

After leaving Leiden, he spent a year at Heidelberg, under Hofmeister. From 1871 to 1875 he taught in Amsterdam, spending his vacations in Würzburg, with Sachs. In 1875, he gave up his position at Amsterdam and took a research position at Würzburg, working on physiological problems connected with crop plants—red clover, potato, sugar beet. He was already interested in the matter of turgor, and it was during this period that he accumulated the data for his first book, a small volume which showed, as the result of much experimentation, the fundamental rôle of turgor in the growth of plants.

In 1877 he became Privat-dozent in Halle, and later in the same year was called to Amsterdam as lecturer in Plant Physiology in the University. The following year he was made Extraordinarius, and in 1886 became Ordinarius in Botany. For the next 32 years he guided the destinies of the Botanical Institute of the University, retiring in 1918 to Lunteren. During this long period he had several calls to other institutions, including one to Columbia University; he preferred, however, to remain in Amsterdam.

He made three trips to the United States. During the first visit, in 1904, he delivered the address at the opening of the Station for Experimental Evolution of the Carnegie Institution of Washington, later gave a convocation address at the University of Chicago, and then spent the summer at the University of California at Berkeley. The lectures which he gave at California were published in book form, under the title "Species and Varieties, their Origin by Mutation."

His second trip was in 1906, during which he again lectured at Berkeley, and gave many lectures in other universities. His final visit was in 1912, when he delivered an address at the opening of the Rice Institute at Houston, Texas.

Many honors were conferred upon de Vries during his long career. He was recipient of the Darwin Medal in 1906, the Veitsch Medal of the Royal Horti-

cultural Society in 1910 and the Linnaean Gold Medal in 1929. Among his honorary degrees were those from Columbia University, University of Chicago, University of Pennsylvania, University of Aberdeen, Cambridge University, University of Berlin, the Landwirtschaftliche Hochschule in Berlin, and the University of Halle. He held membership in more than 50 learned societies, including honorary, corresponding or foreign membership in the following: Royal Academy of Belgium, The Institute of France, German Botanical Society, Prussian Academy of Sciences, Academy of Sciences at Vienna, Royal Society of London, Academie dei Lincei of Rome, Russian Academy, Paris Academy of Sciences, American Philosophical Society, Academy of Natural Sciences in Philadelphia, National Academy of Sciences in Washington, Botanical Society of America, the American Genetic Association. He was honorary associate of the Station for Experimental Evolution of the Carnegie Institution of Washington.

His published writings, up to 1925, exclusive of books, have been collected and published in seven volumes, entitled *Hugo de Vries: Opera e periodicis collata*. The volumes contain 189 papers, and total some 4,300 pages. In addition to his articles, de Vries wrote a number of books, including: *Intracellular Pangenesis*, 1889; *Die Mutations-Theorie*, 1901 and 1903; *Species and Varieties, their Origin by Mutation*, 1905; *Plant Breeding*, 1907; *Gruppenweise Artbildung*, 1913. Besides these, he wrote a textbook of botany and three books dealing with his trips to America, all in Dutch.

Early Experiments

The history of de Vries as an investigator falls naturally into two periods; the earlier devoted chiefly to experimentation in the fields of respiration, growth, turgor and osmosis; the latter to problems of variability, heredity and evolution.

The earlier phases of de Vries' work were of fundamental importance in the development, not only of current conceptions of cell mechanics, but also of physico-chemical theory in general. He began early an intensive study of turgor phenomena in living cells. As a result of exact experimentation in this field, he demonstrated the fundamental importance of turgor in the growth and in the movements of plants. His interest in turgor naturally led him to a study of permeability and the osmotic properties of the living membranes which surround cells. It was in this field that some of his most significant contributions were made. Using living cells as material, and testing a large number of different substances in solution, he determined the exact concentrations of these substances which would just cause plasmolysis or shrinkage of the cells, and which therefore had the same osmotic value as the cell sap. Thus he was able not only to determine the osmotic pressure of the cells, but also to compare the osmotic properties of the various substances used. As a result, he made the fundamental discovery in 1884 that the osmotic pressure produced by a substance depends upon the number of molecules of this substance in a given amount of solution.[2] Solutions of different substances which have the same number of molecules of the solute per liter give the same pressure, or more briefly stated, equimolecular solutions are also isosmotic. This important discovery made it possible to determine the approximate molecular weights of substances by the use of the plasmolytic method. Thus, in 1888, de Vries determined correctly the molecular weight of raffinose, about which there had been some dispute, from a study of its osmotic properties. A much more important result of this discovery, however, was that it made possible van't Hoff's classical conclusion that osmotic pressure and gas pressure are analogous phenomena, and have the same explanation, Boyle's Law applying equally to both.

But de Vries found further that not

all substances follow with strictness the rule that equimolecular solutions are isosmotic; some solutions produce a greater osmotic pressure than is to be expected on the basis of this rule. Analyzing his data carefully, he discovered that substances fall into four classes with respect to the amount of pressure which they will produce, and he established the existence of a simple numerical relation between the relative degrees of activity of these classes. This important further discovery helped to furnish the physical basis upon which Arrhenius formulated in 1887 the celebrated theory of electrolytic dissociation. Thus it is seen that the pioneer researches of de Vries upon the action of osmotic membranes in living cells were of prime importance in the development of two of the most important concepts of modern physical chemistry.

Variability and Mutation

As early as 1880, de Vries began to lecture to his students upon variability, and to take an active interest in the question of the origin of species. Darwinism had by this time won a wide acceptance among biologists, and the origin of species through the gradual accumulation of minute variations was in the way of becoming an orthodox biological doctrine. To de Vries, the experimenter, however, a placid acceptance of a process which no one had actually observed was not easy; what was needed, he felt, was concrete experimental evidence of the actual appearance of new types. Consequently, he began a broad and comprehensive study of the nature of variability, utilizing a number of different approaches. He began the accumulation of an herbarium of sports and monstrosities, and devoted considerable attention and a number of papers to the question of their inheritance and to the effect of environmental conditions upon their appearance and degree of development. He studied with care the effects of selection on the modification of specific characteristics; and he undertook extensive experiments to analyze the variability which is to be observed in the progenies of hybrids. He made extensive field studies to determine the extent and nature of variability in wild species. In all of these lines of study he combined intensive, thorough, painstaking observation and experiment with an extensive range of material. In this way, he accumulated a vast array of facts bearing upon various aspects of the problem of the origin and nature of variations.

Such a program could not fail to yield results, the more important of which may now be mentioned. First, he became early convinced that hereditary characters are separable, and dependent upon distinct morphological entities which are present in the cells. This concept, which he elaborated in a publication entitled "Intracellular Pangenesis" (1889), is of considerable interest to the geneticist, for it foreshadowed in great measure the modern concept of the gene. de Vries assumed the existence, not only in the germ cells, but also in every cell of the body, of one or more morphological structures or pangenes, corresponding to each hereditary characteristic. These bodies are the units of life, all protoplasm being composed of them. The nucleus contains at least one pangene of each kind, but, except for those which govern the activities of the nucleus itself, these are in an "inactive" state. In order to become "active," they must migrate into and become a part of the cytoplasm, whereupon they take on their appropriate activities. In cell division, the pangenes, which are capable of multiplication, divide, and the division products are found in both daughter nuclei. Consequently, every cell in the body has at least one full set of pangenes. Hereditary characters may be altered by (a) alteration in the number of pangenes (a greater number resulting in a greater development of an organ, a reduced number resulting in its reduction), or (b) by modification of a

AMONG THE OENOTHERAS

Figure 1

Dr. de Vries and his wife in the greenhouse which is part of his experimental garden at Lunteren. Here during the last seventeen years of his life he continued his studies of evolution.

pangene. When a modified pangene multiples sufficiently to have a noticeable effect, it alters the characteristic controlled by this pangene. de Vries did not commit himself as to the exact position of the pangenes in the nucleus, but suggested that placing them in the newly discovered chromosomes would be in entire harmony with his concept. This theory represented a considerable advance over Darwin's hypothesis of pangenesis. It is to be judged, not in the light of modern knowledge, but in relation to the state of knowledge at the time of its formulation. When so considered, it is seen to constitute an important progressive step in genetical theory.

A second, and more fundamental result of de Vries' experiments on variability was his discovery of the existence of exact numerical relations between the different classes in the offspring of hybrids, relations which Mendel had discovered previously, but which de Vries, in ignorance of Mendel's papers, worked out independently. Using a wide variety of material, he obtained typical mono-hybrid splitting in Agrostemma, Chelidonium, Coreopsis, Datura, Hyoscyamus, Lychnis, Oenothera, Papaver, Solanum, Trifolium, Veronica, Zea and others. He recognized not only the phenotypic ratios, but also determined correctly the genotypic and back-cross ratios. He obtained, furthermore, di-hybrid phenotypic ratios in at least two cases (Datura and Trifolium), and gave the correct explanation for their occurrence.

After de Vries had obtained and analyzed many of these results, he came across Mendel's publications. This discovery, apparently made early in 1900, stimulated him to publish in brief the results of his crossing experiments, which he did in two short notes,[4 5] in one of which (the first to be submitted for publication, the second to be published), he called attention to Mendel's work. He thus became the first of the three botanists who independently discovered Mendel's papers to get his announcement into print.*

The results of de Vries' breeding experiments, which were thus announced in a preliminary way, were published in full in 1903 in the second volume of his *Mutations theorie*. Through his intensive and keenly analytical studies on plant hybridization, therefore, de Vries succeeded in obtaining, with a wide variety of material, the same results that Mendel had previously obtained with peas, and thus was able to produce convincing confirmation of the correctness of the Mendelian principles, at the very time when these were being brought to the attention of students of heredity.

Experiments with Oenothera

A third result of de Vries' investigations was that they led him to the material and to the observations which eventuated in his celebrated Mutation Theory of Evolution. The material which he cited in support of this theory was varied and extensive, but there was one group of plants which took on an importance far exceeding that of any of the others in this connection, namely, the genus Oenothera; and because the Mutation Theory has been regarded by many as de Vries' most important contribution, the genus Oenothera has been associated in a peculiarly intimate way with his name.

de Vries came upon *Oe. lamarckiana* in 1886, in an abandoned field not far from Amsterdam. In addition to thousands of typical plants, there were here and there in the field aberrant individuals of different types. This suggested that perhaps new species were here in the process of arising from old. Collecting seed he grew many thousands of plants in his own garden, and found the same aberrant types again appearing that had ap-

*The other two discoverers of Mendel's papers, Correns and Tschermak, had also obtained results from breeding experiments similar to those of Mendel.

Photographs by Dr. G. H. Shull

MUTATIONS OF THE EVENING PRIMROSE

Figure 2

Leaf rosettes of *Oenothera lamarckiana* (*A*) and of some mutant types discovered by de Vries in his original investigations of this species (1886-1899). Of the seven mutant types first described by de Vries as appearing in over 50,000 progeny of nine wild plants, four are shown here: *oblonga* (*B*), *gigas* (*D*), *albida* (*E*), and *lata* (*F*). It is now known that *oblonga, albida,* and *lata* are trisomic forms with fifteen chromosomes instead of the fourteen found in *lamarckiana. Gigas* is a tetraploid (28 chromosomes), and *semi-gigas* (*C*) a triploid (21 chromosomes). The cytological explanation of these forms came long after de Vries' initial observations on which his mutation theory of evolution was based.

Photograph by George H. Shull

THE BREVISTYLIS MUTANT

Figure 3

This mutant was one of the first discovered by de Vries. It is characterized chiefly by short styles in contrast to the long styles of *lamarckiana* (right). *Brevistylis* is a gene mutation, and typical mendelian segregation is obtained in crosses, in contrast to the situation in most of the other mutations discovered by de Vries, which are due to more complicated abnormalities of the chromosomes.

peared in the field. Some of these bred true, and seemed possibly to represent the beginnings of new species. He made, therefore, an intensive study of variability in Oenothera and other material, and as a result formulated the Mutation Theory, which suggested that new species arise, not by the slow accumulation of minute variations, as Darwin had postulated, but by sudden, gross changes in the hereditary material, causing sports or mutations, which, if favorable, may represent the beginnings of new races. This theory, while no longer held in its original form, was of great importance, in that it challenged Darwinian authority, and set biologists to thinking along new and fruitful lines.

Shortly after de Vries began to work on mutation in Oenothera, he found this genus to have an additional claim to interest; he found it to be peculiar, not only because of the readiness with which it throws aberrant types, but also because of the fact that it shows certain anomalies in its ordinary breeding behavior. He was at this time already becoming familiar with the fact that pure types breed true, and hybrids give progenies which split according to definite ratios. In Oenothera, however, he found for the most part a different situation: with few exceptions, the various species he worked with, including *lamarckiana*, bred true when selfed or inbred, and thus behaved like pure species; but when crossed with each other, they behaved like hybrids, for they tended to produce, not uniform F_1 families, but more than one kind of F_1 individual; furthermore, the hybrids thus produced often failed to yield splitting progeny, behaving when selfed like pure species. How could pure species produce splitting progenies when crossed? On the other hand, how could hybrids breed true when inbred? This was the anomalous situation which de Vries found in Oenothera. He was able to analyze and explain this situation only partially, but by his investigations he opened up a most interesting field of research which has been abundantly occupied since that time.* Many interesting and important facts have been learned in

*Incidentally, it may be noted that later work on Oenothera has placed de Vries' mutations in an entirely new light. The origin of most of them may now be explained in terms of alterations in chromosome number or in the arrangement and distribution of chromosome segments. The mutants of de Vries do not arise as he thought they did; nevertheless, there is still a possibility that forms produced as some of them are produced, if they breed true, and if they have survival value, may constitute the beginnings of new races.

connection with these investigations, and the anomalies which de Vries found have since been adequately analyzed and interpreted in the light of chromosome behavior of a peculiar type, which most of the Oenotheras possess. This is not the place to enter into a description of later researches in Oenothera; it will be enough to point out that de Vries' initial investigations opened up what has proved to be one of the most fruitful fields of modern genetical research.

It is still too early to measure accurately and fully the significance of de Vries' work. It may be suggested, however, in summary, that his contribution is of special importance in two respects: (1) He was a great pioneer experimenter, opening up important new fields of investigation; (2) he was a vigorous champion of the experimental, as opposed to the speculative, approach to the fundamental problems of heredity and evolution.

As pioneer experimenter, he initiated lines of endeavor which have resulted in some of the most significant of modern biological and physicochemical discoveries and concepts. By his careful analysis of the phenomena of turgor and osmosis, he opened the way for the generalizations of van't Hoff and Arhennius. By means of his hypothesis of intracellular pangenesis, he led the thought of biologists in the direction of the modern conception of the gene. Through his revolt against a placid acceptance of Darwin's idea that new species arise by the slow accumulation of minute variations, and through his attempt to assign to sports and aberrant types their proper rôle in evolution, he began the movement which has led to our present understanding of the nature of genetic change and of the origin of heritable variations. By his painstaking and accurate analysis of the breeding behavior of hybrids, he accumulated a wealth of confirmatory data which helped to make the acceptance of Mendel's postulates, when they were brought to light, an easy matter. Through his study of the breeding behavior of Oenothera, he opened up a fruitful field of investigation, which has led to a number of important results.

But de Vries' work was significant not only because of the discoveries and the ideas contributed, but perhaps even more because of the method exemplified. In championing close and accurate observation and experiment, in an era of speculation, he brought students of heredity and evolution back to earth, taught them the necessity of a strong factual basis for every hypothesis, and in so doing made possible the rapid advance which has characterized this field in recent years. His work has yielded many tangible results of the greatest importance, but above and beyond all such, the intangible influence, arising from his insistence upon experimentation and the patient accumulation of facts, will probably prove to be his greatest and most lasting contribution to biological progress.

During the summers of 1927 and 1928, the writer and his wife worked for some weeks in de Vries' garden at Lunteren. They found themselves the guests of a man of distinguished appearance, of discriminating tastes, of broad sympathy; a kindly man, with a quiet sense of humor, a genial smile, and an unstudied informality of manner that put one quickly at his ease. Amid pastoral surroundings, enjoying the companionship of his gracious and talented wife, happily engaged in carrying on his Oenothera investigations, as well as in breeding new varieties of apples for the Netherlands government, he had become the embodiment of rich and mellow old age. In the weeks thus spent at Lunteren, his guests came to appreciate as deeply the admirable personal qualities of de Vries as they already had learned to value his services as an investigator. It is fitting, therefore, that this appreciation should close with a note of tribute to the rare charm and gracious personality of Hugo de Vries.

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Ralph E. Cleland.

✦

WHITE AND NATIVE CULTURE IN ALASKA

THE production of this book* arose out of recognition of the fact that the white man's school system might not be best for native peoples. The United States Commissioner of Education interested himself in the subject, with the result that the Carnegie Corporation agreed to finance a two-year study of the natives of Alaska, to be made by Dr. Anderson from Stanford University in collaboration with Dr. Eells, the Professor of Education in the same institution.

Dr. Anderson and his wife, who was a trained Binet Intelligence Test examiner and an experienced educational and social worker, spent over a year travelling in Alaska and the Aleutian Islands by every type of conveyance from dog team to aeroplane. They studied not only the Eskimo and Aleuts who constitute two-thirds of the native population, but the Indians as well, directing their attention especially to educational and welfare problems. They travelled some 20,000 miles and Dr. Eells 8,000 miles. The result is a remarkably extensive picture, especially of the Eskimos, as they exist in Alaska today.

The work is divided into two parts; I. A sociological study of the Alaska Eskimos, II. An educational study of the Alaska natives. The government is conducting school and community work in 48 Eskimo villages with a population of over 7,000. Thirty-two of these villages were visited. Similar work is being done in 14 Aleut villages having a population of 1,120, and in 30 Tinneh Indian villages (population 5,817).

Without being primarily anthropological in their outlook, the authors have incorporated in their work a summary of what is known with regard to the origin, habitat, physical appearance and material possessions of the Eskimos in this region, as well as a short history of their contact with white peoples, which began in 1728 with the voyages of Behring. Statements regarding the former conditions of the Alaskan Eskimos are mainly taken from Murdoch (1892) and Nelson (1899). Various anthropometric measurements were made, and numerous measurements and tests of fundamental abilities and educational achievements are recorded.

A chapter is devoted to the extent and effect of contact with whites. It is suggested that every fourth person in the native population is of mixed blood; but of 58 families, supposed pure, which were measured, thirty-four were revealed as having white blood, showing that much early diffusion of white blood also took place without being recognized. Probably the extensive taking of the

*Anderson, H. Dewey and Eels, W. C. *Alaska Natives.* A Survey of Their Sociological and Educational Status. Stanford University Press. 1935. $5.00.

blood groups would give the best measure of admixture, but this has not been done. It is especially desirable that the Aleuts should be blood-grouped before it is too late.

These writers, like nearly all others, testify to the liveliness, good nature, friendliness and intelligence of the Eskimos, in marked contrast to the general psychology of the Indians. From the Seashore musical tests it appears that they, as well as the Indians and especially the Aleuts, rank low in musical ability. The Alaskan Eskimos, while speaking one language, are divided, primarily by dialects, into eighteen tribes. It appears that they have largely given up shamanism and adopted the white man's religion. The native type of igloo is largely replaced by wooden huts, food habits are being much altered, but skin clothing is necessary in winter for all dwellers in this region. The introduction and multiplication of reindeer has been an advantage, but the export of reindeer meat and skins has not yet become an important industry.

Part II is a detailed study of the school conditions, educational methods and health of the Eskimos. Perhaps of greatest interest in this connection are the results of intelligence tests and the measurements of fundamental abilities in the school children, grouped into numerous tables and graphs. The relation of I.Q. to race, purity of race, degree of contact with white civilization, years of school attendance and age of child, are tabulated. It is concluded that the mental ability of Eskimo children is distinctly inferior to that of white children in the United States, that it increases regularly with increments of white blood, that it is not perceptibly affected by contact with white civilization, by age or by school attendance, but that some allowance should be made for the linguistic features of the Binet Scale tests. The authors emphasize that the lower intelligence level should be reflected in the school curriculum and teaching methods adopted. Specific recommendations to the number of 124 were made, bearing on every respect of the educational work in Alaska. This survey will no doubt have a marked influence on such work. The recommendations appear to be well-considered and the whole is an important contribution to the educational problems of primitive peoples.

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BLOOD WILL TELL

IT has been six years since a comprehensive monograph on the blood groups has appeared in English. During these years much intensive work has been carried out on this subject, particularly on the new *M* and *N* reactions and the sub-groups of group *A*. In this volume* Dr. Wiener has brought together in readable style all of the recent advances in the principles and practical applications of blood grouping. Especially valuable are the careful descriptions of technics: methods of preparing and titrating serums, sources and elimination of errors, technic of transfusion, and methods of applying the medico-legal tests.

Academic phases of the problem have not been omitted. Biometrics and genetics fundamental to a proper understanding of blood groupings are briefly but adequately discussed. Anthropological investigations are summarized. Individual differences in animal bloods are analyzed and compared with the human blood groups.

Finally the specific problems of medico-legal applications are carefully presented and elaborated. Of especial interest are the case histories, the résumé of the legal status of the tests in various parts of the world, and the identification of stains, both of blood and other substances.

Laurence H. Snyder

*Wiener, Alexander S. Blood Groups and Blood Transfusion. Pp. xiv + 220. $4.00. Springfield, Charles C. Thomas, 1935.

EFFECTS OF FEMALE SEX HORMONE ON PLUMAGE COLOR

The Influence of Female Sex Hormone on the Expression of Plumage Color Genes in Crossbred Fowls

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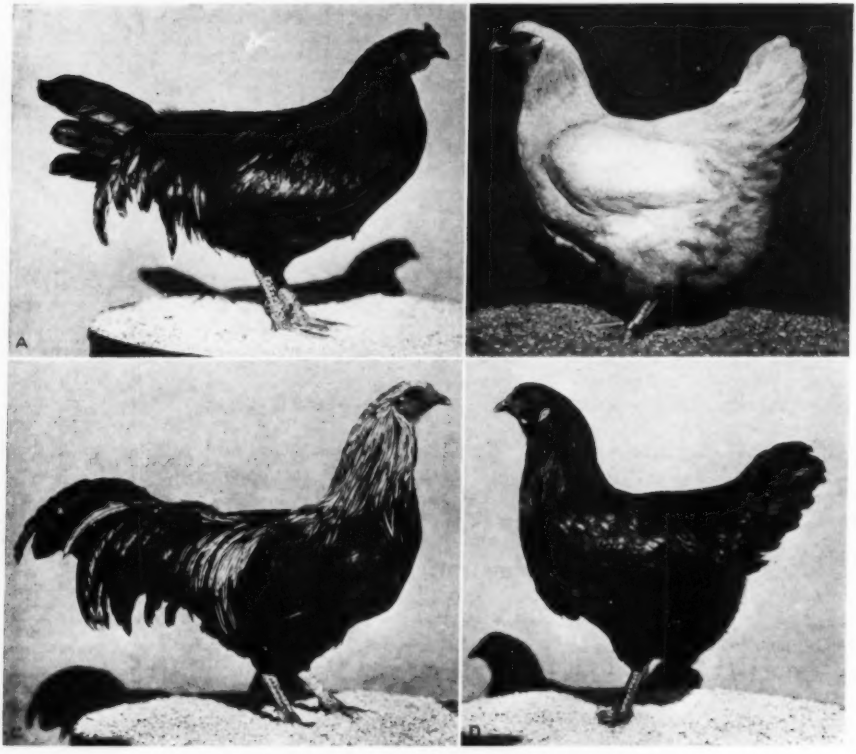
THE sexual dimorphism in coloration commonly observed among certain breeds and varieties of standardbred fowls is a phenomenon which also appears quite frequently among certain crossbreds. In the adult plumage of the progeny of a Black Spanish × White Silkie cross, Darwin[2] noted that the F_1 males had red* hackles, shoulders and saddles whereas the F_1 females were black. Some years later, Davenport[3] pointed out that the F_1 males from black × gold crosses carried red on the wing-bow, saddle and hackle and that the F_1 females were solid black. In several crosses among the recessive white breeds kept at the U. S. Animal Husbandry Experiment Station, Beltsville, Maryland, the F_1 males were reddish in wing-bows and the F_1 females were pure white. Various theories have been offered to account for this phenomenon, one of which ascribes the dimorphism to sex linkage and another to the influence of the female sex hormone.

Effect of Sex Hormones

The appearance of red in certain crossbred males and its absence in females of the same parentage might be due to a difference in genetic constitution, involving a sex-linked gene. In a black × gold cross, for example, the F_1 males, *ssEe*, receive a double dose of gold, *ss*, whereas the F_1 females, *s-Ee*, only get a single dose, *s-*. Jull and Quinn[4] observed red lacing in the hackle, red on the shoulders and red lacing in the saddle of F_1 black males from a cross of Rose-Comb Black Bantam male × Rose-Comb White Bantam female, whereas the females were black. They stated that the red color observed in the F_1 black males was sex-*linked*. However if this were true, the F_1 black males should have transmitted the red lacing to their black F_2 daughters as well as to their sons, but this did not occur. The dimorphism in the F_1 progeny of the Rose-Comb Black × Rose-Comb White cross may have been sex-*limited*, in which case the lack of the red lacing in the F_1 females probably was due to the influence of the ovarian hormone.

Several workers have demonstrated that the sexual dimorphism of the Brown Leghorn variety of fowl is due to the influence of the sex hormone. More recently a few similar tests have been made with crossbred fowls. Caridroit and Regnier[1] suggested that the ovaries of the F_1 black females from a silver × gold cross had properties of melanization. Taylor[7] concluded that the female sex hormone in a Minorca × Hamburg cross made the extension of black pigmentation possible. Regnier[6] demonstrated that the presence of the gene for red color was essential for the production of that color and that ovariectomy resulted in the appearance of a color only when that color was genetically present. These investigations seemed to indicate the effectiveness of sex hormones in determining certain crossbred genotypes. Consequently, it was desired to study

*The terms red, red color, non-silver and gold have been used by various authors to designate the genes involved in reddish plumage color and, therefore, are used synonymously throughout this article.



SEX DIFFERENCES IN COLOR EXPRESSION

Figure 4

In the cross of black Sumatra male (*A*) × White Wyandotte female (*B*) the first generation chicks are all black. The F_1 males (*C*) later develop silver and gold pigmentation in hackle and saddle feathers but the females (*D*) remain black. It is demonstrated that this difference is not due to a sex-linked gene but is the result of an effect on the pigment-forming mechanism by the sex hormones. Injection of the F_1 male with the female sex hormone produces solid black plumage and removal of the ovary produces red or silver pigment in the female plumage.

the effect of the female sex hormone on Beltsville crossbreds, using for this purpose an aqueous solution of theelin.

A suitable cross was found in the mating of a Black Sumatra male × White Wyandotte females. In this cross all of the F_1 progeny were black in down color at hatching time. At about four months of age, however, the F_1 black males began to show silver and gold in the hackle and saddle whereas the F_1 females were, without exception, solid black. There was not the slightest evidence of red splashing or ticking anywhere in the plumage of the F_1 females. More than 100 of these F_1 black females were observed and all of them were as black as purebred Black Sumatra females. (See Figure 4 *D*.)

In certain other black × recessive white crosses made at Beltsville, some of the F_1 black females showed a slight evidence of red color in the plumage of the throat and the upper part of the breast, but the F_1 black females from the Black Sumatra × White Wyandotte mating showed no sign of red color.

EFFECTS OF SEX HORMONE INJECTION

Figure 5

Feathers from a caponized F_1 male of the cross of Sumatra × White Wyandotte. *A* shows the normal color pattern in the male; *B* shows the widening of the black central stripe produced by injection of 550 units of theelin. When this dose is increased to 2100 units the feather pattern shown at *C* is produced. Note the black bar toward the tip. The pigmentation is produced at a certain definite stage in the development of the feather. If the theelin treatment were begun soon enough and continued long enough the entire feather would be solid black. It is possible by such use of hormone injections to determine in a few weeks whether a sex difference in plumage color is due to genetic causes or to action of the sex hormones.

In order to determine whether or not the sexual dimorphism was produced by differences in sex hormones, it was decided to change an F_1 black female (Black Sumatra male × White Wyandotte female) into a poulard by ovariectomy, and to feminize* one or two of the F_1 black males (Black Sumatra male × White Wyandotte female), which showed brassy silver in their hackles, wing bars, and saddles. In feminizing the F_1 males it was desired to establish an effective dosage of theelin in an aqueous solution. It was also desired to determine, by the changes obtained in plumage, the genotype of the F_1 black female.

It was supposed that the F_1 black-silver males (which were brothers) had obtained the sex-linked silver gene from their White Wyandotte dam. As a matter of fact, the genotype of this White Wyandotte dam was a matter of record. She had been previously tested with a Rhode Island Red male, which mating showed that she carried the sex-linked gene for silver. The F_1 black female, however, did not receive the sex-linked silver gene from her Wyandotte dam, and, consequently, could be either a silver or a non-silver, depending on her Black Sumatra sire, whose genotype was unknown.

Ovariectomy of a four-month old F_2 black female resulted in a change from the female to the male type of plumage and the appearance of red plumage color in the wing bows and saddle of the resulting poulards. This change was completed within sixty days. The result demonstrated that the F_1 female of this cross was a potential gold, *s-Ee*, and did not carry silver. Also that the Black Sumatra sire carried the gene for non-silver. The Black Sumatra sire, however, may not have been pure for the non-silver genes, as he could have been either *SsEE* or *ssEE*. Since one positive experiment was sufficient to show that the gold was genetically present in the F_1 black female, further efforts were directed toward the feminization of the F_1 males.

Two of the F_1 black males which showed silver and gold lacing in hackle and saddle were caponized. One of these proved to be a slip. The saddle feathers were plucked from both capon and slip, and when the new quills protruded from the sheath, one cubic centimeter of theelin (aqueous solution) was injected. At the time the injections were made the weights of the F_1 males averaged about 1,600 grams, the capon weighing 1,605 grams and the slip 1,590 grams. The dosage of the aqueous solution required to produce a noticeable effect on the silver plumage was not known. Mitchell[5], working with Brown Leghorn capons, found that 150 rat units of theelin a day (saline solution), given in three injections, were required to produce a barely noticeable change in the color of the mid-portion of the feather, changing it from male type to female type. The smallest amount of theelin necessary to return a positive growth reaction of the vaginal wall of a spayed female rat is recognized as one rat unit. In the present experiment, a dosage was desired which would effect a complete change in color as a result of the injection. This was found to be 450 rat units in three doses of 150 rat units each during any 24 hour period, or three times Mitchell's dosage.

Dosage

The first trial of 400 rat units of an aqueous solution of theelin given in two doses, 250 rat units and 150 rat units respectively, had no noticeable effect on the growing plumage of the plucked bird. A dosage of 450 rat units given in three injections over a period of 24 hours gave a noticeable effect. After a sufficient lapse of time the procedure was repeated with 550 rat units of theelin given in doses of 250, 150, and 150 units over a 24-hour

*The term feminize has been used to express the process of causing capons to take on female plumage. This is usually done by the injection of female hormone or by grafting on ovarian tissue.

period. This treatment caused a definite widening of the black stripe along the midline of the feather, as shown in Figure 5 *B*. A large black bar was produced in the silver and gold lacing of the same birds when doses of 150 rat units of the aqueous solution were injected three times daily for four and two-thirds days. This total of 2,100 rat units caused the large black bar shown in Figure 5 *C*.

The effect of the injection of theelin is not immediately apparent, since the part of the feather affected is buried in the sheath. About two weeks' time is required for the feather to grow sufficiently to expose this portion. The black bar shown in Figure 5 *C* was about one centimeter long and, as can be observed, effectively covered the silver lacing of that portion of the feather where it appeared. Undoubtedly, continued injections of theelin would have caused the disappearance of the silver entirely, resulting in a totally black feather.

In addition to the change in color of plumage the usual change in feather shape was induced by the injection of female hormone. This can be seen by comparing the more rounded tips of the feather in Figure 5, *B* and *C* with the relatively pointed tip of the feather in Figure 5 *A*. A similar change in feather structure was shown in hackle, and wing bar. The change in pigmentation was associated with the change in feather structure, from the characteristic pointed male feather to the more rounded form of the characteristic female feather.

Summary

It has been shown by ovariectomy that the F_1 black female (Black Sumatra male $\times$ White Wyandotte female) carried red color, since the removal of the ovary allowed this red color to appear in the shoulders and saddle. The aqueous solution of theelin changed the silver and gold of the F_1 males to black. Since the female hormone has been shown to influence both silver and gold, it is concluded that the F_1 female did not carry silver since silver did not appear after ovariectomy. This is in accordance with the theoretical genetic constitution of the bird.

Whether or not a genetic dimorphism is determined by gonadal secretions can be ascertained within a few weeks by the hormone test without resorting to a breeding test, which would extend over a longer period of time and would involve the expense of rearing large numbers of offspring.

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GENETICS IN 1935

IN a youthful subject like genetics, where growth is rapid and conceptions are continually changing, it is highly desirable that new textbooks should appear from time to time. They serve as an historical record of the development of the subject. Moreover, each new work invariably has

some point of excellence, even though it may not merit high praise as a whole. My own collection of texts is nearly complete, and I have yet to find one which is not helpful. Either it serves a different grade of students, or is especially clear on certain points, or presents new illustrations, or opens up novel problems, or cites better examples than those that had been used previously.

Snyder's new book* is no exception. It is written with extraordinary clearness and with a commendable brevity. In fact, the reader may be inclined to criticize the short shrift that the author has given to subjects which extend to a score or more of pages in other textbooks. Yet further consideration usually shows that a more extended exposition would be unnecessary and confusing. The chapter on the cytological basis of crossing over is a good illustration. In it Snyder shows a real genius for lucid writing.

Several excellent texts on genetic principles have been published, but those which can be heartily recommended require substantial biological preparation. There is a need for a book which can be understood by students who have no more of an acquaintance with biological matters than comes from a half-year of the elements of the subject. In the opinion of the reviewer, this work will fill the vacancy. Some fairly abstruse topics are considered; but they are discussed so well, with all technical words explained in passing, that the serious student who fails to grasp the meaning may be fairly rated as having less than average intelligence.

There are numerous new examples and new illustrations which the teacher will find useful in the classroom. As might be expected, since the author is a zoologist, these citations tend to be too exclusively from animal genetics; but this is not important. The reviewer recommends the book to all teachers who wish an authoritative up-to-date work for use by the beginning student. Many lay readers will also find it valuable.

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Bussey Institution

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THE DAYLILIES

IN ten chapters plus a preface and an appendix, Dr. Stout brings together in an interesting, and scientific manner, most of what is known about the fashionable and popular daylily group.* He has grown and studied them for over twenty years himself, during which he has brought together at the New York Botanical Garden, one of the largest and most complete collections of varieties and species of these beautiful ornamentals. Much of his information is drawn from this background and hence has the advantage of being first-hand, which tends towards greater accuracy since he has been there, and knows the plants.

Full detailed descriptions of the various species and their varieties, with practical points on their uses and culture are given. The volume is copiously illustrated with photographs, drawings and colored plates. There is an index, a selected list of daylily literature, and an address roll of individuals and firms who have been conspicuous in the development, breeding and dissemination of the more recent types of daylilies. Special chapters consider the evaluation of the numerous types, propagation, the names, and a historical retrospect. If one is interested in daylilies, this is undoubtedly the book to have.

Orland E. White

University of Virginia

*Stout, A. B., *Daylilies*s The wild species and garden clones, both old and new, of the genus *Hemerocallis*. Pp. X + 119. 1934. Price $3.00. The Macmillan Co. New York.

INVALIDATION OF THE GENETIC EVIDENCE FOR BRANCHED CHROMONEMAS

In the Case of the Pale Translocation in Drosophila*

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Status of the Problem

ONE of the most firmly established principles of biology is that of the linear arrangement of genes in the chromosome and of the linearity of the chromonema which (as the second author stated in 1916[14]), must form the physical basis of the linear linkage map. Expressed in terms of the individual gene, this means a bipolar gene structure, with a consequent bipolar method of attachment of the genes to one another.[15] That the unidimensional arrangement of genes holds even on the finest genetic scale possible, i. e., in the case of directly adjacent genes, can be deduced in the case of Bar genes from the results of Sturtevant's experiments on unequal crossing over[27] and is substantiated by recent work of Muller and Prokofyeva[19] on the arrangement of genes in the region of the scute locus.

There has for a long time, however, existed one apparently contrary genetic finding, which challenged the universality of the linear principle. This is the case of "Pale translocation" in *Drosophila melanogaster*, which has been interpreted as probably involving a branched chromosome structure. In this case, the first translocation known to genetics, it has been concluded—to quote from the last account given of Pale translocation, by Morgan, Bridges and Schultz, in December, 1932—that: "The original Pale-translocation (1917, 1923) involved a break of chromosome II at about the locus of plexus, and the lateral attachment of this terminal fragment to the third chromosome at about the locus of Hairless." The translocated piece was thus supposed to be attached to the side of the third chromosome, in a non-terminal position, and presumably it was attached at its point of breakage. The attachment, whatever its nature, was found to be quite stable, in that the piece does not tend to become lost from the chromosome to which it is affixed. The door having once been opened, by this case, to the principle of branching, another case recently found in Drosophila, which seems genetically similar to the first, has been interpreted in the same way.[6]

It will be seen that if any interpretation involving the conception of some sort of side-attachment in these cases is correct, the principle of bipolar gene connections and of a linear gene order must be violated at the locus or loci where the branch is attached to the main part of the chromonema. For this locus, the radically new principle must be admitted, that a gene may somehow develop an extra attachment point. The gene must then be supposed, not only to be capable of self-duplication in this new form, but to be capable of just the right kind of self-duplication in order to insure that the other new genes in the daughter chromonema that is formed will also have the same method of tripartite at-

*Transmitted for publication Nov. 22, 1934. It should be explained that the present work was carried out in May, 1934, and written up soon afterwards, though publication was delayed by a number of circumstances.

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tachment to one another at this locus as in the mother chromonema. In terms of chromosome "division," this is equivalent to saying that the plane of "division" must pass exactly through the point of side-attachment; more accurately, we should say that the plane of self-duplication must be parallel to the plane passing through all three points of gene attachment of a tripolar gene. Further than that, in the separation of the two branched structures from one another, there must be no tendency to breakage. If, now, such tripartite or multipartite structures can exist and be thus inherited in quite stable fashion, it is hard to see why they should not, in the course of evolution, have become more and more numerous, until at the present time the chromonemal structure should have become many-branched or netlike, or have lost all semblance of linearity. Since the latter has not been the case, we should be all the more cautious about accepting the interpretation of a stable branched structure.

In recent years a series of cytological observations has been reported (see Darlington,[4] Levan,[8] Mather[9]) in which branched chromosome structures have actually been seen, and they have been interpreted (especially the case of Levan's) according to the precedent set by Pale translocation. For the reasons stated above, it will be very important to push the analysis of such cases further, so as to demonstrate conclusively the existence of an actually branched *chromonema*. If we admit that such exists here, however, we must also determine the degree of stability of this structure in the course of mitosis and meiosis, and solve the problem of why a structure of this kind is never found in established condition in normal material. For it is quite conceivable that the principle of bipolar attachment may sometimes be violated, but that such a violation is only at the cost of some genetic instability or disharmony.

Whatever discoveries may later be made along this line, it is evident that the finding of new facts in connection with the original cases may also be helpful. It is the purpose of the present paper to bring forward new evidence which proves the falsity of the interpretation of Pale above given, and brings it precisely into line with the orthodox linear principle. In the process of reinterpretation, moreover, certain considerations arise which tend to throw doubt also upon the interpretation of the later genetic case in Drosophila.

It may be instructive, in our consideration of the case of Pale, to pass in review first the earlier work, which eventually led to the conclusion that the gene-string was branched, and then to present our more recent findings.

Earlier Work on Pale Translocation

In the winter of 1917-18 Bridges found what was apparently a dominant diluter of eosin eye color, which had at the same time a lethal action, regarded by Bridges[1] as gametic. This lethal "gene" seemed to be located in the second chromosome, and the really startling fact in connection with it was that there seemed to have arisen at the same time, in the third chromosome, another gene, itself lethal or partly lethal, that acted as a "suppressor" of the first lethal, and was in turn "suppressed" by the latter. This curious coincidence was communicated by Bridges and Sturtevant to Altenburg and Muller for suggestions. Altenburg immediately pointed out that the series of phenomena found their natural explanation in the supposition that a piece of the second or third chromosome had become broken off, causing a deficiency there which would have a lethal effect, and had become attached to the other chromosome (third or second), where the extra fragment would have the effect of suppressing this very lethal; at the same time the effect of the extra fragment would itself tend to be lethal, unless compensated by the de-

ficiency. For this phenomenon, no case of which had hitherto been encountered, Altenburg proposed the term "transposition" (later modified to "translocation" by Bridges).

Arguments were then advanced by Muller to show that the observed simultaneous origination of such exactly complementary effects could not well have any other interpretation than that given by Altenburg, and he designed a series of crosses for a demonstration and further analysis of the matter, including a study of the expected changes in linkage relationships of known genes in the second and third chromosomes and of the expected "covering" action which the normal genes in the attached fragment would have upon recessives in the second chromosome. At the same time, being sceptical of a gametic lethal effect, he designed a series of crosses, with markers, to show that individuals could be produced which had received the deficiency only from one gamete and the attached fragment only from the other gamete, and that therefore the lethal action of the deficiency, unaccompanied by the fragment, was only on the zygotes and not on the gametes. These series of crosses were carried through exactly according to plan by Bridges, and gave the expected proof of Altenburg's explanation of the case, as well as of the zygotic action of the lethal; they supplied in addition various details concerning the chromosomal configuration involved, the new linkage values, and the relative viabilities of the various possible zygotic classes.[1, 2] Later tests, by Muller and Settles,[20] proved that the deficient and the over-stocked gametes, when aged or X-rayed, retained as high a viability as the normal ones—a result which they explained by the non-functioning of the genes in the spermatozoa; this result completely precluded any gamete-lethal action.

The above linkage experiments of Bridges showed that a section of the second chromosome, about six to eight linkage units long, lying apparently at the extreme right end, had been removed. The break had occurred between the locus of arc, at 99.5, and that of plexus, at 99.8, all tested loci that lay to the right of arc being included in the section that had been removed. Among those known to be thus included may be mentioned, in addition to the locus of plexus, those of lethal IIa, brown eye, purploid, morula, speck, blistered and balloon; the last is the rightmost gene known in chromosome II. The fragment of chromosome II, containing the normal allelomorphs of all these genes, was shown by its linkage relationships with the genes in the third chromosome to be attached to that chromosome at about locus 80($\pm$5), about half way between ebony and rough, (though not at Hairless as stated in the quotation previously given). That is, it is attached near the middle of the right half of the genetic map of the third chromosome, the exact point being uncertain owing to the reduction of crossing over caused by the presence of the extra fragment in heterozygous condition. The non-terminal position of the attached piece was a matter for considerable surprise and naturally led to the supposition that it might be attached branchwise. Cytological observations were then made by Bridges that at first gave negative results, the piece being apparently too small to be seen by the methods then in use.

On account of the important point of principle that would be involved in a real violation of linear gene arrangement, it was desirable to seek for alternative explanations, together with tests thereof. It was pointed out by Muller that the idea of side-attachment itself included such different sub-possibilities as side-attachment of the fragment merely at its breakage point, branchwise, or adhesion of the fragment along its whole length to the side of the recipient chromosome, but that, as an alternative to any scheme of side attachment at all, the

piece might have become *inserted into* the third chromosome in linear fashion, at a point of breakage of the latter, one of the surfaces or "points" of fracture of the third chromosome having become attached to one end of the fragment, and the other surface of fracture of the third chromosome to the other end of the fragment. In order to decide between these two major possibilities, he suggested to Hamlett a study of the linkage values of genes in the third chromosome, in individuals both of whose third chromosomes carried the translocated piece. If the latter were inserted linearly, the linkage map should then be lengthened, inasmuch as genes such as ebony and rough, which lie on opposite sides of the insertion, would have become spread further apart thereby. In the heterozygous individuals on the other hand, reduced crossing over frequencies had already been observed between these genes, but that was to be expected even in the case of an insertion, owing to the non-matching of the two conjugating elements; the real test then would come only in the homozygotes. Now Hamlett's test seemed to show as low a frequency of crossing over between ebony and rough, in the individuals homozygous for the translocation, as in the heterozygous ones previously studied, and he accordingly concluded that the piece was not inserted but somehow attached to the side, in a way that interfered with crossing over even in the individuals homozygous for it.

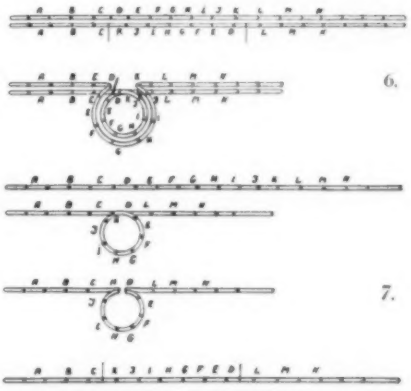
This result cannot however be regarded as a definite one, for the test was subject both to great technical difficulties and to error in the interpretation, as the viability and the fertility of individuals homozygous for the attached piece is ordinarily very low. A complicated scheme of crossings had had to be carried through, utilizing various markers in special ways, to make possible the detection of these homozygous individuals, and if an error had crept in at any point, a combination of artificial and natural selection would have favored the obtaining of individuals heterozygous for the translocation, but showing the desired somatic characters, and these individuals would of course have exhibited the already known linkage variation. This work, therefore, deserves careful repetition. It may be observed, however, that even in case the crossover frequency in the homozygote were proved to be lower than in the normal, this fact would not necessarily disprove the insertion explanation, since these individuals all carry a third representative of the region in question, on one of their second chromosomes (flies homozygous for the deficient second chromosomes always die, even when homozygous for the attached piece on the third), and the second chromosome may thus enter in, through its synaptic attraction, to disturb the conjugation between the third chromosomes.

If the insertion interpretation were correct, it might be expected that some of the translocations obtained in the X-ray work would be found to involve insertion. Proof of this matter, however, ordinarily requires a special genetic analysis, including (as attempted above) a study of crossing over in the form homozygous for the rearrangement, while at the same time heterozygous for genes in the region of the disturbance. Considerable technical difficulties are here involved, since most rearrangements disturb viability or fertility when homozygous, and when heterozygous reduce crossing over so as to hinder the introduction of desired genes into the regions in question. In the first years of the X-ray mutation work, therefore, this matter could not be settled.

The first definitive evidence of insertion was obtained by Oliver[23] in the Texas laboratory. In his case, chromosome III was broken between curled and stripe, and again between ebony and claret, the section between these two breaks acting genetically as though attached to the *X* chromosome near echinus. As Oliver re-

ported, "presumably the *X* chromosome became broken at this point to allow the insertion. Cytological observations show a shortened III and a lengthened *X*, but no indication of a branched structure. Crossing over occurs between the shortened III and a normal III on either side of the fracture, and between the lengthened *X* and a normal *X* on both sides of the insertion, but is characteristically affected in frequency." Another case probably also involving insertion was described by Oliver at the same time. Study in greater detail, by Offermann and Muller,[22] of the case of translocation X-IV, 1 (first recorded by Muller and Stone[21]) showed that this too involved an insertion in which, surprisingly enough, the tiny fourth chromosome had become broken and had had inserted into it a large piece that had become deleted from out of the *X* chromosome. Finally, in a parallel paper, Muller[17] (1935, in press) describes almost the complementary type of insertional phenomenon to this, in the case of scute 19, in which a fragment that would in the ordinary metaphase chromosome be ultramicroscopic, has become deleted from the *X* and inserted into the large second chromosome at a non-terminal point, namely at about locus 13, a unit to the right of the locus of Truncate.

In view of these proved cases of insertions produced by X-rays, the insertion hypothesis for the natural translocation known as "Pale" received further plausibility. In the meantime, some further observations which had been made by Bridges on Pale translocation, both from the cytological and the genetic side, had made a final solution of this case more urgent. It was reported by Bridges[12] that he had apparently discerned a slight difference between the length of the normal second chromosome and of that having the Pale deficiency; at that time he classified the third chromosome as being normally longer than the second. Somewhat later,[13] on the basis of renewed observations, he announced that an effect of the



CONJUGATION OF NORMAL AND INVERTED CHROMOSOMES

Figures 6 and 7

These drawings show schematically the results of conjugation of two chromosomes, one of which carries an inversion in the central region (D-K). The lower half of Figure 6 shows in diagram this material as it appears in the chromosomes of the salivary gland. Figure 7 shows schematically how these chromosomes produce the results shown in Figure 6. The two loops differ in that one of them might be called a "direct loop" and the other an "inverted loop." When these two loops are fused they result in a configuration in which each band in one chromosome is paired with its homologue in the other chromosome just as is the case when two normal chromosomes conjugate without the formation of a loop.

translocation was discernible on the lengths of both the second and the third chromosomes, but at the same time he reversed his previous conclusions as to the lengths of the latter, when normal, with respect to each other. In regard to the last point, the still later conclusion of Dobzhansky[5] disagreed with his, while that of Muller and Painter[18] agreed. Thus the whole matter was again thrown into doubt. If, however, the length of the third chromosome was visibly affected, as claimed by Bridges, it would seem that the case must be one of insertion rather than side-attachment.

On the other hand, Bridges (in the report of Morgan, Bridges and Schultz[10]) soon afterwards announced genetic results which, on the insertion

view, would be surprising. The work was based on large counts of progeny of individuals heterozygous for the translocation and for markers in the region of the second chromosome subject to the translocation. The counts showed that a minute amount of crossing over does occur between the attached piece and the homologous region of a normally arranged second chromosome. The crossover combinations observed were such as to agree with the assumption that the piece was attached at its broken end, to the side of the third chromosome. If it were inserted, these crossovers could only be explained as double crossovers, in which both points of double crossing over had occurred within the inserted region, and since the latter was normally only six to eight units long, and here much less on account of the reduction of crossing over frequency in individuals with heterozygous translocations, the possibility of double crossing over would, at first sight, seem one hardly to be entertained. These results, then, would seem to make the case strong again for the idea of non-linear arrangement, which, as our earlier quotation shows, was the one then accepted by the group in question.

The Cytological Resolution of Pale Translocation

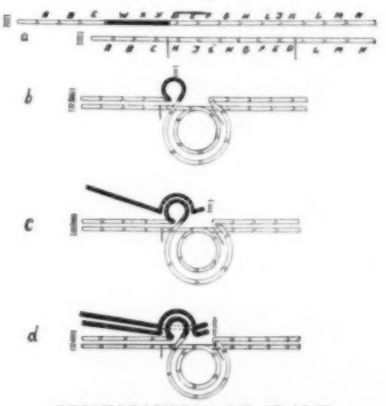
It was thought that all these questions might be decided definitely and simply if a study of the structure of this translocation were made in the chromosomes of the salivary glands which, according to the well-known work of Painter,[24, 25] show the details of chromosome morphology about 100 times more extended than do the ordinary metaphase chromosomes. For this purpose it was advisable to use individuals heterozygous for the translocation, since the figures formed by the synapsis of the homologous regions of the translocational and non-translocational chromosomes would then more clearly show the structure of the rearrangement. It was also desirable to have some sign by which the right half of the third chromosome could be specially marked, cytologically, in order that attention might be focussed on this most critical region. A balanced stock was therefore made up, in which the right arm of one of the third chromosomes contained the well-known inversion, "CIIIP" (=InP), but not the attached piece of Pale translocation, and the other third chromosome contained the attached piece but had an otherwise normal arrangement of genes, while the second chromosomes were heterozygous for the Pale deficiency but otherwise had normally arranged genes. As a result of the heterozygous inversion in the right arm of the third chromosome, we should expect a loop to be formed on this arm. The formation of a loop, attached by a kind of chiasma figure in one region to the rest of the chromosome pair, is a regular occurrence resulting from the presence of heterozygous inversions in the chromosomes of the salivary glands, since this is the necessary consequence of a conjugation of all homologous loci. The reader may convince himself of this on perusal of Figure 6, which shows in purely schematic fashion the complete conjugation, such as occurs in the salivary glands, of two chromosomes, one of which carries an inversion. The expected loop was, in fact, found in our CIIIP material, and served readily to mark the right arm of the third chromosome as desired.

It was to be expected that within the loop representing the inversion, or not far from it, the attached fragment would be found, either as a side-attachment or as a piece interpolated in one of the homologues and not found in the other. It was found, as a matter of fact, at a point almost opposite the right (distal) end of the inversion, and so near to the attachment of the loop as ordinarily to come within the chiasma-like figure formed by the shifting of partnership of the chromosomes (see Figures 8 and 10). It is clear in all the figures examined that this extra piece is not attached to the

side in any way, but forms an integral part of the chromosome in which it lies, which thereby becomes quite noticeably lengthened. This leaves no doubt at all that the insertion hypothesis is the correct one.

On the other hand, the inserted piece is so small, relatively to the whole chromosome, that we do not believe it would ordinarily make a detectable difference in the length of the chromosome, as seen in metaphase figures. This helps to account for the mutually contradictory character of Bridges' two sets of reported results concerning the relative lengths of the second and third chromosomes, based on the idea that Pale translocation could be used to mark them. In metaphase figures, moreover, the chromosomes may vary so much in their relative condensation that the normal second chromosome sometimes appears larger than the normal third, and sometimes smaller.

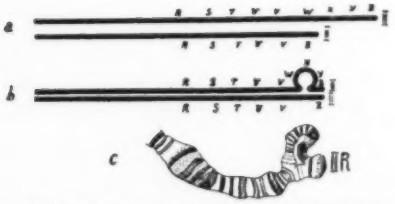
One difficulty with the insertion hypothesis not above mentioned had been the fact that it seemed in this case to require that one of the surfaces (or "points") of fracture of the third chromosome became attached to the unbroken right hand terminus of the second chromosome, while the deficient second chromosome meanwhile acquired a new termination, coinciding with one of its own surfaces of fracture. More recent evidence indicates that the attachment of pieces to the very end of a chromosome, rather than to another breakage point (or "surface of fracture"), rarely or never occurs, and that it is equally rare, at least in the case of "active" regions, for a chromosome to become simply broken off, with the broken end serving as a new terminal point. A study of the present case, as seen in the chromosomes of the salivary glands, showed that these rare conditions did not obtain here. For observation of the right arm of the second chromosome revealed not only that one homologue was shorter than the other by an amount equal to the size of the extra piece in one of the third chromosomes, but that the deficiency in question was not quite terminal in its position. This is well shown in Figure 9. The very ends of the right arms of the two second chromosomes are here in conjugation, as well as most of the length of these



CONJUGATION OF "PALE TRANSLOCATION"

Figure 8

In the pale translocation a portion of the second chromosome has been transferred to the third chromosome. This is shown schematically at *a*, in which the translocated region (W-Y) is black. When a strain heterozygous for this pale translocation is mated with a strain containing the well known "CIIIP" inversion a situation is produced at conjugation in which a double loop is formed as shown at *b*. In this the translocated part of the second chromosome is not synapsed and represents an unpaired strand. An actual case of this type as seen under the microscope is shown in Figure 10. At *c* is shown a more complicated situation in which the normal "right arm" of chromosome II is in conjugation with the homologous region inserted as the "pale translocation" into the third chromosome. An actual case of this type is shown in Figure 11. At *d* is shown conjugation further complicated by the fact that the second chromosome is paired, one member of the pair being normal and in part conjugated with chromosome three as in *c* and for the rest conjugated with the deficient second chromosome. This results in synapsis of all homologous parts of the chromosomes in question, and is readily explicable if the underlying factors are understood, but very complicated if these are unknown. This situation is shown in actual microscopical material in Figure 12.



SYNAPSIS OF NORMAL AND DEFICIENT SECOND CHROMOSOMES
Figure 9

This shows at *a* the schematic representation of a normal second chromosome and a second chromosome having the "pale deficiency." Synapsis of these forms is shown at *b*. Here the deleted region is represented by a loop in that part of the normal chromosome which is deleted in its mate. *c* shows a microscopical preparation as seen in salivary gland material. The looped, unpaired strand with band-by-band synapsis on either side of the deletion, can be clearly seen.

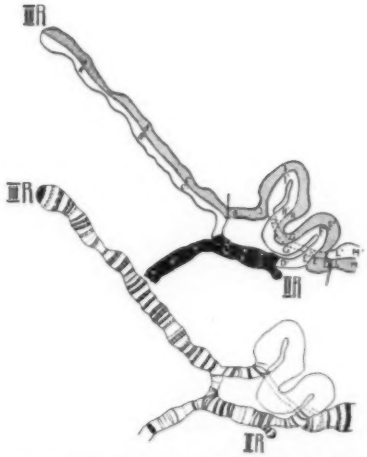
CONJUGATION OF INVERTED AND "PALE TRANSLOCATION" THIRD CHROMOSOMES
Figure 10

This drawing of a microscopic preparation of the salivary gland chromosomes, showing conjugation of the paired third chromosomes each of which contains known abnormalities, is shown schematically in Figure 8*b*. The "CIIIP inversion" has resulted in a large loop (shown in outline only), and the "pale translocation" is represented by a smaller loop. The unsynapsed loop of the second chromosomes is shown opposite the longer loop represented by the inverted part of the third chromosome.

arms, and the region which does not match lies near, but not quite at, the end, so that the normal chromosome, when it conjugates with the shortened one in both regions that correspond has to buckle in the region between, in respect to which the other chromosome is deficient. This is a usual phenomenon observed in salivary gland chromosomes in cases of deficiency (or, generally speaking, in any cases where one of two otherwise homologous chromosomes contains a non-terminal region not represented in the other; this would include cases of "insertion" as well as those of "deficiency").

It was further to be observed, in various cases, that the region of the normal second chromosome which found no partner in the deficient second chromosome, had come into conjugation with the inserted piece in the third chromosome, so that a complicated figure was formed, as shown in Figures 8*c* and 11. This latter connection served as a complete confirmation of the whole insertion interpretation, by proving that the extra piece to be seen in the third chromosome really had been derived from the second chromosome, through the deletion of the latter. The arrangement of parts further shows unmistakably that the translocated part of chromosome II has become attached in an inverted position, in the sense that that end of it which was previously nearer the spindle fibre is now further from it, while, of course, the end which was further is now nearer.

In Figure 12, finally (as in the schematic Figure 8*d*), all the above points are demonstrated at once, since we observe all the rearranged homologous parts in conjugation simultaneously: namely, the inverted and the homologous non-inverted parts of chromosome III, forming the loop; the translocated (and simultaneously inverted) and the homologous normally arranged parts of chromosome II; and also the parts of II lying on either side of the deleted region. In none of these figures, moreover, is there any evidence that any materials had become removed from the third chromosome, in a reciprocal fashion, and inserted into the second chromosome in the region of the deficiency of that chromosome, as would have happened if the process of translocation had involved merely a kind of illegitimate double crossing over between the sec-



SYNAPSIS OF PALE TRANSLOCATION WITH SECOND CHROMOSOMES

Figure 11

This situation is shown diagrammatically in Figure 8*C*. The lower part of this figure shows a drawing of the actual microscopic preparation and above an interpretation of this in diagrammatic form. Here the part translocated from the normal second chromosome is in synapsis with the second chromosome, while the inverted part of the third chromosome is represented by a large loop distinct from the loop due to the pale translocation.

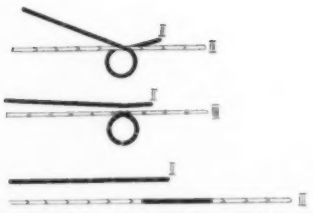
CONJUGATION OF TRANSLOCATED AND DELETED CHROMOSOMES

Figure 12

The lower figure is a drawing of the microscopic preparation and the upper figure is a diagrammatic interpretation of this. The situation is shown in schematic form in Figure 8*d*. In this two pairs of second and third chromosomes are involved—the third chromosomes, carrying respectively a "CIIIP inversion" and a "pale translocation," and the second chromosomes being normal and "pale deficient." Unless the genetic situation were understood such a figure would seem meaninglessly complicated. It is possible by the use of salivary gland chromosome material to observe under the microscope the types of configuration expected on the basis of genetic presuppositions, and thus to obtain direct observational evidence regarding the correctness of one or another genetic interpretation.

ond and third chromosomes.

It *seems* too much to suppose that the three breakages which appeared in the present case had no connection with one another (see Muller, 1932). Nevertheless we have just seen that they probably did not follow the usual rule of crossovers, according to which breakage and recombination occur at any given point simply between *two* strands that presumably lie across one another. Here it seemed that there must have been three strands, all touching one another at exactly the same point, as shown schematically in Figure 13. It would seem a curious coincidence that a third strand should touch at precisely that point at which two other strands are already touching, as this hypothesis would seem to require. Yet we have even better evidence for the same kind of principle in the case of scute 19, where it is certain, on genetic grounds, that no active material was transferred from the second chromosome to the *X*, although a piece deleted from the *X* became inserted into the second.[17] In obviation of the difficulty created by the non-mutual character of these insertions and by the consequent inference that three chromosome regions must have met at one point, it has been suggested by Offermann that two of the regions may have happened to lie across one another at



A SUGGESTED MECHANISM FOR PRODUCING DELETIONS AND TRANSLOCATIONS

Figure 13

This figure shows a schematic representation of the manner in which a deletion-insertion such as the "pale translocation" might occur. The same result as that here shown might, alternatively, have been produced if the chromosomes had not originally been looped as shown, but had accidentally become broken at the same points as those here indicated (i.e., at the points here represented as intersection points) and had at a later time come into contact and adhered together at their points of fracture, so as to give rise to the new arrangement of segments. Which of the two possible mechanisms is correct we do not yet know.

first, and that the third strand may then have slid along them until it became caught exactly in the notch made by the crossing of the first two, thus allowing the occurrence of the complicated interchange of the type found. The alternative is to suppose the breaks to have occurred independently of one another, and for the contacts and reunions to have occurred later.

Bearing on Other Cases and Discussion of Related Problems

The above proof of the insertional character of Pale translocation carries a number of implications which have a bearing on any similar cases supposed to involve side-attachment. For the present case has been the best studied one of this type. Its disproof of side-attachment thus calls very seriously into question the validity of the side-attachment interpretation of any other cases which have only been studied genetically. Genetically it is now not enough to show that a region which *seems* to include the end of the genetic map of one chromosome has become attached to another chromosome in a non-terminal position, since this was true in the case of Pale. The translocation described by Dobzhansky and Sturtevant[6] as a case of side attachment had, to be sure, the feature that some crossing over occurred between the genes of the translocated piece and those of the homologous region of the normal chromosome; these were of such a nature (including cases where only the originally more terminal genes of the fragment had separated from the other genes, and never cases where only the proximal genes had separated from the others) as to indicate that the piece was attached only at its broken end. It will be recalled, however, that very similar results had also been reported by Bridges in the case of Pale translocation, and must now be interpreted as due to rare double crossing over. That interference is unusually low in the end regions of chromosome II is indicated by results of Spencer.[26] Since, moreover, in just the case of Sturtevant and Dobzhansky here under discussion, the authors state that their numbers were small and irregular, and they do not give the exact data concerning their findings, it is hard to see how crucial this evidence was. A reexamination of this case would now be highly desirable.

The cytologically reported cases of branched chromosomes are of course on a different footing. Levan's case seems to be particularly well founded. Yet here too it would seem desirable to pursue the analysis further in several directions: (1) what is the state of the actual chromonema, at the supposed point of branching, as seen in stages when the chromosome is extended? (2) what happens to the branched region during the pachytene and diplotene stages? (3) how stable is the structure through mitosis and, in general, through sexual reproduction? It must be realized that there is no genetic precedent here, and that

the finding and intensive study, both cytologically and genetically, of actually branched chromonemata, would, for reasons stated in our preliminary discussion, be of exceptional theoretical interest, because of the bearing of such facts upon questions of the structure of the gene. Among these questions are: to what extent may the gene depart from a bipolar structure, and how may such a departure interfere with the gene in its self-duplication and other normal operations.

We already know, of course, that the genes which form the natural free termini of the chromosomes act as unipolar. There is reason, however, based on certain translocations being studied by us, to believe that in some cases at least this unipolarity covers a latent or potential bipolarity, since a portion of the chromonema derived from elsewhere may apparently become attached to the very end of a chromosome. The converse of this s e e m s also to occur occasionally, though very rarely: namely, that an interstitial gene, with bipolar attachment, becomes terminal and thus unipolar. In the case of loci within or bordering on the inert region, the latter sort of change occurs much more frequently (results of Levit, quoted by Muller,[16] and since corroborated in experiments of the latter).

A further fact of interest concerning the two attachment poles of the gene is that they are of the same general nature, that is, not opposite in sign or having a "lock and key" relationship. This is shown by the occurrence of inversions, for if the two poles of a gene had different signs ("north" and "south"), then, at the points of breakage and reattachment of the inversion, north pole would have had to become joined to north pole, and south to south, so to speak.

Though the gene is so minute, it must ultimately be considered on a much magnified scale, and it must be recognized that it has not only poles but different "faces," the properties of which must certainly differ from one another. There is already reason to believe, from the two-by-two method of conjugation which chromatids usually follow at synapsis, that a specific face exercises a specific kind of attracting force, and that the chromatids probably conjugate face to face. Otherwise it would seem that they would be able to conjugate in indefinite succession. In the salivary glands, where the chromatids do practically line up in indefinite succession, in the curved surface of the periphery of a cylinder, it has been noticed by Muller that there is nevertheless some indication that, at times at least, they are grouped in pairs within this surface. This would mean that, besides the specific attraction exerted directly between the faces of major attractive force, there is (especially in Diptera) considerable residual attraction, exerted in the same plane; the latter must operate upon (or, at any rate, through) the "back" surfaces (i. e., those opposite to the surfaces of strongest attraction).

Presumably the most direct attraction operates between the mother gene and the daughter gene that is constructed in the image of the former. Strange to say, this does not seem to result in a mirror image, for if it did there would exist allelomorphs, and in fact whole chromosomes, of two opposite signs. In conjugation, these would react differentially with one another—especially in triploids. The lack of such a distinction shows that, if face-to-face attraction is really the rule, then there can be no differentiation of the attractive forces, or of their determining structures, in a direction transverse to the chromonema (at right angles to the longitudinal and the front-to-back directions).

Although such questions are not directly touched on by the present work, which concerns only the "polar" connections, i. e., those between adjacent non-homologous genes in the same chromonema, nevertheless this whole complex of problems is closely interrelated, and they must eventual-

ly be considered in connection with one another, if we are to arrive at an adequate understanding of gene structure.

Summary

1. Proof has been obtained that, in the case of Pale translocation, the fragment which was removed from the second chromosome did not become attached to the side of the third chromosome, as had been supposed, but became inserted within the length of the third chromosome without any disturbance of the principle of linear gene arrangement.

2. The fragment of the second chromosome in question was not a terminal fragment, but was deleted out of the second chromosome, near the end, by means of two breaks of the second chromosome; the very end segment became again attached to the remainder of the chromosome. The deleted piece became inserted into the third chromosome, in inverted position, at a point where the latter had become broken. Thus attachment took place only between broken ends ("surfaces of fracture").

3. The observations of the chromosomes in the salivary glands, which enabled proof of the above points to be obtained, showed conjugation (varying in degree) between all homologous regions of the normal and rearranged chromosomes, resulting in the complex figures to be expected for such rearrangements.

4. Despite the transfer of material from chromosome II to III, there was no perceptible reciprocal transfer of material from III to II, as happens in double crossing over. This indicates that at precisely the point of breakage three chromosome regions met one another. The latter condition seems to require the assumption of the catching of strands at points of crossing of other strands; as Offermann suggests, such an effect might be mechanical. Alternatively, we should have to suppose that breaks occurred independently of contacts, and that reattachment occurred subsequently.

5. The cytological evidence presented extends the hitherto known limits of the second chromosome, by proving the existence of a section of it lying to the right of the rightmost gene hitherto known (balloon).

6. The crossovers which had seemed to show that the translocated fragment was attached at only one end must therefore have in reality been double crossovers in which both points of crossing over occurred between the two points of attachment of the fragment. As the latter are not more than 8 units apart (when in the normal chromosome), these double crossovers span a much shorter distance than was hitherto thought possible for double crossovers in any region lying entirely on one side of a spindle fibre attachment.

7. In view of the fact that the genetic evidence for side-attachment in the present case appeared to be stronger than that in any other known case, great caution should be exercised in drawing conclusions of side-attachment in other cases that have been investigated only by genetic methods and show similar peculiarities in their heredity. At the same time, apparent cytological cases deserve especially searching investigation, since any which really involved a branched structure would illustrate new possibilities of gene behavior that might be significant in considerations of gene structure.

8. Various problems concerned with the polar attachments and the facial attractions between genes are discussed.

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Effect of Age at Marriage on Size of Family

ONE of the reasons why increasing increments of education tend to reduce the size of family has been held to be that increasing age has a markedly depressant effect on fertility. Exact information regarding the extent of this factor has been rather scanty, and additions to it are to be welcomed. The *Journal of the American Medical Association* for May 25, 1935 (Volume 104, Number 21, page 1919) gives a summary of a study made of German statistics by Münzer and Löer bearing on this point. The data presented in the form of a summary table* show the percentage of women of any given age who will ever give birth to a child during the remainder of their reproductive lives.

It is clear that little effect on ultimate fecundity results in this group from marriages occurring before an age of twenty-three or twenty-four. Seven years later prospects of children are just 50% as good. Ten years later, or at age thirty-three, the average prospects

* See next page.

of ever giving birth to a child are less than a quarter as great. Münzer and Löhr also present data on the number of children the women in the group studied were likely to give birth to at various ages. At the beginning of the fertility period this number was, in 1931, only 1.72 children. At age eighteen this figure also begins to drop and at age forty-five the value reaches 0.01. (These figures refer to the women who have actually given birth to one or more children, not to the entire number of women.)

The note which presents these figures gives no indication of the size of the population on which they are based. If they are typical it is clear that a few years' difference in age at marriage is of itself enough to account for most of the differential birth rate. No information is given as to the percentage of this increasing sterility which is voluntary and the percentage which is due to causes beyond the control of the individual. On that point depends much of the effectiveness of the efforts to increase the birth rate such as those now being put forth in Germany and Italy. It has been brought out recently in the *Journal* that most of the recent German increase in births has been due to a large number of first children, and that this ripple of births is a direct result of a wave of marriages encouraged by intensive propaganda and by cash bonuses. It is pointed out in this study "that the biological probability, to judge from the statistics on marriages, would doubtless be much higher even for the women of the older age group." If this is so, effective propaganda might bring about some increase in size of families. It is out of the question to hope long to delay the impending decline in population merely by increasing the number of one-child families.

In proportion as this increasing sterility is involuntary it is obvious that the most (and perhaps the only) effective way to increase the number of children per married couple is to reduce the age at marriage. From this it follows that one of the major objectives of a program of positive eugenics to correct the differential birth rate must depend on practical methods of encouraging early marriage in the better endowed fraction of the population. Here eugenists are presented with a problem of applied economics that will tax their ingenuity in "social invention" to the utmost.

The Percentage of Women Who, Having Had No Children, Will Give Birth to a Child
After Munzer and Löhr

Age	Percentage to Bear Children	Age	Percentage to Bear Children
15	68	31	25
16	68	32	21
17	68	33	17
18	68	35	11
19	67	34	14
20	66	36	9
21	65	37	7
22	63	38	5
23	61	39	4
24	58	40	3
25	54	41	1.8
26	50	42	1.1
27	45	43	0.7
28	40	44	0.4
29	35	45	0.2
30	30		

R. C.

A Bibliography of Research in Sex Differences

THE *Psychological Bulletin* for May, 1933 (Volume 32, No. 5, page 343-354), contains an annotated summary of recent research and discussion of sex differences in man. The bibliography contains 121 references ranging from Mrs. Roosevelt's "It's Up to the Women" to Van de Velde's "Sex Hostility in Marriage." This field of research and speculation is not one in which objective conclusions are easily reached. Thus the author accepts the "Lili" case as an authentic instance of sex reversal in man. Reasons for considering this case very unsatisfactory and inconclusive were given in this JOURNAL some months ago (Vol. 25, pp. 67-69). In spite of this rather uncritical treatment the summary shall be valuable for those wishing to obtain recent references to literature in this field.

MAN'S PROSPECTS AND RETROSPECTS

Reviewing Some Recent Discussions of Homo Sapien's Future Extent, Present Arrangements, and Early Development

AND AFTER US—?

*THE Twilight of Parenthood** is the best written book on population, from the literary standpoint, that has yet appeared. It abounds in provocative and picturesque sentences: "Malthus provided an attractive rationalization for the imperfections of a *laissez-faire* economy . . . A false antithesis between sex and food flattered the vanity of the undersexed and the overfed." "The present crisis of underconsumption is the nemesis of imposing a planned ecology on a planless economy." "The Jewish food ritual illustrates the way in which mankind imposes what Anatole France calls the 'arbitrary limitations of religion' upon the selective processes of Nature. The ox may have engaging attributes which commend it to the Psalmist, but the rabbit, the oyster, and the pig—none of which is Kosher—have vastly greater thermodynamic potentialities."

A rich variety of materials have been drawn from ecological, economic, and demographic studies for this construction. And these materials have, for the most part, been purposefully used, although more or less irrelevant bits of information also appear in the final structure, the drayman having apparently brow-beaten the architect.

The book has a definite and challenging thesis: "The conclusion which emerges most clearly from our study is that the *laissez-faire* economy is a biologically self-destructive arrangement of man's social life." "The crucial problem of maintaining the reproductive vitality of civilization is how to reinstate the child as a functional unit in a planned ecology."

And the answer, insofar as the author defines an answer, is found in certain actual changes in the U.S.S.R. and certain other possible aspects of socialistic economy. This thesis is developed in a fashion that is always imaginative and often convincing.

Finally, Miss Charles has a remarkable facility for presenting statistics with accuracy and with lucidity, although she makes no original statistical contributions in this work. For the student, the book affords a pleasant and valuable introduction to modern demographic techniques.

Too Many—or too Few?

The work is, however, largely dominated by strong emotional drives not originally derived, one suspects, from objective population studies. Though scornful of the "Jeremiahs of overpopulation," she proclaims the "menace of underpopulation" in the best prophetic style. It becomes rather difficult to find the exact significance of such a metaphor as the following: "When a sports car is rushing downhill without brakes, it is no comfort to be told that the scenery may be more delightful a few yards further on. The crash at the bottom is our first concern."

In the survey of world population trends, the two-fifths of us who live in India and China are dismissed with the inaccurate assumption, "These populations are more or less stable." Our author points out, with regard to the situation in Japan, that although there are signs of the beginning of birth rate decline, rapid population increase continued in England for two generations after the birth rate began to drop. And

*CHARLES, ENID. *The Twilight of Parenthood.* Price, $2.50. W. W. Norton, New York, 1935.

she expects population increase in Russia, indefinitely. It will be a long time before the human race again reaches the modest number of individuals living at the beginning of the eighteenth century—and they, if neatly arranged, would after all make up quite a jolly company. Surely we shall have many aeons to experiment with new ways of living before we become as rare as Neanderthals or buffaloes. "The crash" is hardly just ahead. Of course, those who believe that a decline in the number of Nordics would bring on a cultural ice age have better cause for neurasthenia—but Miss Charles eschews such ideas as chauvinistic. We must all grant that no society can be accepted as permanently satisfactory that does not become self-replacing, so the real problem of the book remains. But if we refuse to be frightened by bogeys and metaphorical catastrophes, we can deal with this problem somewhat more deliberately.

As an answer to "Mr. Keynes' pronouncement that we could maintain a higher standard of living if we had fewer to employ and fewer to feed in the midst of the abundance which applied biological science can now guarantee," our author replies, "Is it more than an admission that deductive political economy is unable to regulate man's social environment by new discoveries and inventions?" The reviewer must confess that he fails to see the logical contradiction between the hypothesis (1) that at a given level of productivity (even such a level as that envisioned in the dreams of the technocrat) a decrease in population below a specified number within a specified economic area might cause an increase in average level of living and the hypothesis (2) that productivity could be raised by further application of scientific discoveries—but the validity of such a contradiction is one of the fundamental assumptions of the book. "Verily, the logician is hard to please," as Miss Charles proclaims in another connection, in the paragraph just cited.

Similarly, in discussing differential reproduction, the author counters eugenic dogmas that seem to her to have their bases in prejudices savoring of fascism with assumptions that are more congenial to her own prejudices, which have a broader and more humanistic basis—rather than by really objective examination of relevant data. She hastily embraces the thesis, supported by very inadequate evidence that, "The pronounced differential fertility, which existed in the early years of the twentieth century and evoked so much eugenic speculation and propaganda was a temporary and exceptional phenomenon." She ignores the few really critical studies of group variations in intelligence (including that by Evelyn Lawrence, published in the monograph series of the *British Journal of Psychology,* in 1931). She speculates, "It may be that the most conspicuous effect of promotion by the scholarship system is to sift out the introverts, and we cannot dismiss the possibility that the introverted type is on the whole less fertile than the extravert." She adds an apology that seems inadequate, although it may be accurate, "If such considerations are admittedly speculative, they are at least no more speculative than the assertions which have prompted them." She then adduces evidence "on a small scale" from "a recent investigation into the employment careers of a group of Hoxton boys." Much as the reviewer may share some of the author's enthusiasms and resentments, he cannot but regret that she failed to lift the discussion on this important subject to a higher level of scientific objectivity.

Which Way Out?

If one accepts the author's main thesis that recent population trends afford new evidence of the unsatisfactory economic and social foundations of Western Civilization, the moral may be pointed toward communism, or toward fascism, or toward liberal reconstruction. It is wholly conceivable that from the strictly demographic point of view an adequate solution might be

worked out along any of these divergent lines of social-economic development. The argument from demography appears conclusive only as advanced against a purely individualistic *"laissez-faire"* economy. The type of response worked out by different individuals and by different peoples to social maladjustments, including unhealthy population trends, will be determined by many different interests. At this juncture it is the function of the demographer, as such, to show the influence of social conditions on population trends as imaginatively, as impartially, and as accurately as possible. In Miss Charles's presentation, the limited role here assigned to the demographer is subordinated to her enthusiasm for a particular social philosophy—or, at least, so it seems to this reviewer—so that, in the first place, the real problem with which she deals is overstated for rhetorical effect, and in the second place, alternative solutions to this problem are not adequately developed.

In any case, whether or not our reservations are justified, this book is one that should be widely read. It ploughs deeply into the sterile soil of complacency, and stimulates vigorous thinking. It should create new interest in population studies.

FRANK LORIMER.

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THE FAMILY

THIS comparatively large volume* is an attempt "to integrate the various scientific approaches to the study of family phenomena." It is a study of the aspects of anthropology, ethnology, psychology, history, sociology, economics and psychiatry, which lend themselves to the formulation of a "unitary science of the family." The subject matter is presented from the "cultural" point of view and analyzed in terms of historical development and cultural change with its effects upon the contemporary problems of family life, and organization.

Part I presents an extensive comparative description of family patterns utilizing the family system of the Trobrianders as compared with American society, various aspects of love and personality formation, and universal patterns of love and personality formations. Part II gives the cultural history and geography of the family, with chapters on prehistory and ethnology, and the history of various family patterns, as developed in different parts of the world. Part III treats of the processes of social change describing the influences of mechanical invention, biological developments and psychological discovery upon the evolution and modern status of society. Part IV contains a comprehensive descriptive account of family problems involving reproduction, care of children, marriage complexities, the divorce situation and the influence of love mores. Part V presents the more pathological features in family disorganization, marital failures, frustrations and parent-child relationships, and Part VI, the final section of the subject matter, outlines the concepts regarding the future of the family system.

The book is crammed with the results of experiments and observations in the field of social psychology, and is rich in stimulating ideas. The appendix presents a long list of "suggested research projects," which could be developed into valuable procedures if subjected to the laws of a rigid methodology. The text is well adapted to stu-

*FOLSOM, JOSEPH KIRK, The Family: Its Sociology and Social Psychiatry. Pp. 604. New York: John Wiley & Sons. London: Chapman & Hall. 1934.

dent use with a selected bibliography at the end of each chapter, a name index and a final subject index. One is left with the impression that the main facts and concepts relating to family organization from a very large field have been presented in a systematic manner.

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MAN'S ANCESTORS

DOCTOR CLARK, who is Professor Elect of Anatomy in the University of Oxford, has executed a detailed and eminently authoritative piece of work on the evolutionary origin of the primates, including man, the results of which are set forth with great clarity in the volume under review.* The style is lucid and, while of necessity including much of a highly technical character, the presentation is such that one finds the volume readily comprehensible and very readable.

The chapter headings give the scope of the book and testify to the completeness of the investigation. The introductory chapter presents the general problem with some of the arguments and beliefs which have ben held, especially the evolutionary laws which have been invoked. Chapter II deals with the distribution of the primates in space and time, while Chapters III to IX speak of the evidences for primate evolution and relationships from the skull, teeth, limbs, brain, special senses, and the digestive and reproductive systems. Chapter X treats of the relation of the existing tree-shrews, generally included in the order Insectivora, to the primates, while the final chapter discusses, with diagrams, the evolutionary radiations of the primates. Some of the author's conclusions are set forth in the following excerpts:

> In the primate skull, almost all of the distinguishing features are due to the progressive tendency towards an enlargement of the brain, a high development of the mechanism of vision with a corresponding reduction in the apparatus of smell, the adoption to various degrees of an upright position of the trunk in locomotion, and the use of the forelimb for prehension rather than for progression, all of which characters are directly associated with an arboreal mode of life. The development of bony crests on the skull depends upon the relation between the muscles of the jaws and neck and the surface area of the neurocranium, so that they occur both in small primate skulls, where the brain is small, and in large skulls, like that of the gorilla, in which the muscles are massive. Such structures do not necessarily indicate the degree of affinity.

Within the primates, all stages are represented between a typical claw and a flat nail, the latter being a degenerative formation which is associated with the increasing importance of the terminal digital pad. The latter not only provides a more efficient grasping mechanism for animals which find it necessary to indulge in arboreal acrobatics, but also becomes a tactile organ of a high degree of sensitivity, aiding in the cultivation of the faculties of perception and judgment. The evidences of the foot structure very convincingly indicate that the forerunners of the Hominidae diverged from the forerunners of the large anthropoid apes at a point of evolutionary time when the common ancestor had not exceeded the body size of the gibbon. The close similarities between man and the gorilla do not necessarily show a close affinity in the sense that man is directly derived from the ancestral stock of the African apes:

> It may (and probably does) only indicate that the gorilla and man have been derived from a fairly distant common ancestor not

*Clark, W. E. Legros, *Early Forerunners of Man.* Price $5.00. William Wood and Co., Baltimore. 1934.

larger than the gibbon, and from which common potentialities and tendencies for evolutionary development have been inherited. * * * Corresponding degrees of resemblance between the giant anthropoids and man need not preclude the probability of their diphyletic origin from a stage of evolution represented by the gibbon (or even * * * at an earlier stage).

The acquisition of the capacity for stereoscopic vision is of extreme importance in the phylogenetic emergence of the higher primates, but the dominance of this sense is apparently correlated with retrograde changes affecting not only the olfactory but also the auditory sense:

In lower Primates, however, the external ear retains the primitive elaboration which is found in most other mammals, for the reason that a nocturnal mode of life necessarily demands considerable auditory acuity.

The tree-shrews are commonly classified as members of the Insectivora. Evidence which is here reviewed shows that in many features they afford rather marked structural contrasts with the insectivores generally, and at the same time display evidence of affinities with the primates. If the comparative anatomy of the Lemuriformes is considered a detail, it appears certain that this group of primates passed through a stage, in its phylogenetic history, which must have resembled the tree-shrews so closely in all fundamental details that no systematist could avoid classifying them in the same super-family—Tupaioidea.

The author concludes that:

The Platyrrhines, Catarrhine monkeys, and Anthropomorpha had become separated at least by the beginning of Oligocene times, and not improbably at an earlier stage during the Eocene period. * * * The latter stages in man's evolutionary history are represented by fossils * * * which have corroborated in a most remarkable way the inferences drawn by anatomists from the study of the structure of man and the anthropoid apes. Such paleontological evidence leads inevitably to the conclusion that the progenitors of the Hominidae * * * must have possessed features * * * by which they would be quite consistently referred to the category of the anthropomorphous apes.

Clearly, the parallelism which has been noted in the Primates is merely an expression of the thesis that the descendants of a common ancestor always tend to evolve similar lines. [These] instances of parallelism in the evolution of the Primates which have been brought to light in the preceding chapters are to be interpreted satisfactorily only by the conception of definite predetermined trends of development—that is, by the conception of Orthogenesis. That conception puts the onus of evolutionary progress more on the germ-plasm and regards the influence of the environment as of somewhat secondary importance. Hence it seems to intensify the mysteries of the germ-plasm, which (it implies) is endowed from the beginning with countless potentialities for evolution in definite directions. * * * If the mysteries of the living and evolving germ-plasm are even deeper and more enigmatical than we have been inclined to believe, it were better to recognize the fact.

Many books have been written on the evolution of man. This volume differs from them all in the scope of the evidence and the judicial manner of its evaluation.

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HUMAN HEREDITY FOR THE LAYMAN

THE reviewer has read with enjoyment this book* of information "for the citizen, who, though not considered capable of managing his own drinking amusements and family affairs, is now consulted on such issues as the international gold standard, the prevention of poverty and the cure of mental deficiency."

Mr. Moore, who has been successively chief officer of the Imperial Bureau of Animal Genetics and editor of the *Eugenics Review*, writes in the language of the English country side, presenting the rules of genetics in terms of horses and dogs and barn-yard stock. There is no labouring with the laity about "bristle," "cut," "dachs," "scute"

*MOORE, ELDON. *Heredity—Mainly Human.* 337 pp., 17 figs. with ten in color. 15 s. Chapman & Hall Ltd., London. 1934.

and the other cryptic verbal shorthand of Drosophila genetics. The style is clear and sparkling, amply suited to express the significance of heredity in determining the I.Q. of one's children or the probable winner of a horse race, (of the latter he says, "Don't try it").

This book deals in an authoritative manner with practical questions such as: the effect of children on slums as well as the effect of slums upon children; the fecundity of defectives which is their chief asset (as it is of other lower forms) in the struggle for survival; the prospects for an adopted child in a good home, and the biologist's opinion of the "Nordic myth."

Only one subject draws forth his adverse comments, and that is Pearl's attempt in the *American Mercury* to minimize the aristocracy of the gene. Moore himself introduces a few speculations on the relation of endocrines to asthma, tuberculosis and cancer, which are not calculated to win the confidence of medical readers. On other topics the information is recent and accurate.

Heredity—Mainly Human, is a book that would grace the library table of a friend. By expressing the attitude of a biologist to human affairs it should do much to dispel the phantasies of literary physicists, who have had remarkable success in "selling" to a large public "island universes" and other objects and concepts so remote that they can have no possible effect on our world or our race for thousands of generations—if then.

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STERILIZATION IN 1934

EXCERPTS from the Report of the Board of Directors of the Human Betterment Foundation for 1934:

During the past year a large part of the resources of the Foundation has been devoted to a second survey of sterilization in California, in collaboration with the California Bureau of Juvenile Research. The task of collecting case histories from the state institutions was completed by the Foundation workers, and all of these were tabulated and coded. Hollerith cards were then punched for each individual, 67 facts being thus recorded for each of about 8,000 persons. These cards are now being sorted to make 1,500 scatter diagrams, which will reveal the correlations of all of the facts. Males and females are tabulated separately, as are also the insane and feeble-minded. In this immense but highly important task, the staff of the Foundation has been helped by six SERA workers furnished by the Bureau of Juvenile Research. The study should be completed within the next year, and will not merely bring up to date the previous study which this Foundation made (beginning in 1926), but will extend it and result in a great deal of new and valuable information.

A great deal of time has been devoted to a continued study of the needed changes in the California sterilization laws, and the President has worked out a bill which would revise the present statutes and undoubtedly give California the best sterilization law in existence.

The biennial tabulation of sterilization statistics from the entire United States is now under way. While this is a slow and laborious undertaking, returns already indicate that there has been a definite and marked increase in the use of sterilization laws during the past two years.

Sweden and Norway have adopted sterilization laws during the past year, bringing the total number of people living under such laws up to more than 160,000,000. The administration of the German law has been slow, but very successful so far as can be judged.

Among outstanding events of interest in the United States is the championing of sterilization by Mrs. Grace Poole, former president of the National Federation of Women's Clubs, and Mrs. John M. Phillips, President of the Pennsylvania State Federation of Women's Clubs.

In California, the administration of the sterilization laws has continued uninterruptedly. The fall election brought into office a new Director of the Department of State Institutions, Barry Lutgens of San Rafael, who is intelligently interested in and entirely favorable to the administration of the law.

HYBRIDIZATION OF COFFEE

A Preliminary Study of Flowering Habits, and of Methods of Crossing

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COFFEE was introduced from the Guyanas into the northern states of Brazil in the year of 1727. During the two succeeding centuries this plant became the main economic resource of the country. Extending southwards, it established itself most successfully in the state of São Paulo where the conditions of soil and climate were best suited to the plant. In this state alone approximately a billion and a half coffee shrubs are under cultivation. This represents a little over half of the entire coffee plantings in Brazil, which total some two billion, nine hundred million plants. Curiously enough these enormous plantings, covering an area of approximately 8.8 millions of acres were established practically without any help or guidance from agronomists and research workers. It was only at the beginning of the twentieth century that Dafert (founder of this Institute and author of many excellent publications on coffee culture) initiated here a large working program mostly concerned with the study of the fertilizing of coffee plantations and other agronomic problems. About ten years ago the officials of this Institute engaged themselves in a new research program to solve the manifold problems of coffee culture. Fertilizer and shading experiments were made and variety and pruning tests were established. The taxonomy, genetics, and cytology of our coffee varieties are being investigated and these researches are to serve as a basis for a large breeding project. A great deal of work is also carried on by state and federal agents to improve the quality of coffee by improving methods of picking and handling green coffee, etc.

The bulk of the coffee grown in Brazil is represented by *Coffea arabica typica*. The variety generally grown is called among farmers "café commum" or "café Nacional." In some districts of the state of São Paulo one finds also another variety, "Bourbon" coffee, which is distinguished from the "Nacional" by its different growing habit, leaf and fruit shape. A third variety, the "Maragogipe" originated by mutation in the state of Bahia in 1876. This variety is characterized by much larger leaves, flowers, fruits, and seeds, but it has not been widely substituted for the commonly grown varieties on account of its low productivity. Besides these three varieties several others have been introduced into Brazil, and still others have originated here by mutation, making a total of over twenty-five recognized varieties at the present time. The cytology of most of these forms has already been investigated by the writer[3]. They are double diploids with $2n = 44$ chromosomes; the basic chromosome number of the genus Coffea is eleven; some of the other species have only $2n = 22$ chromosomes. In future publications a detailed account will be given of these closely related subjects.

In 1932 the Genetics Department of the Instituto Agronomico of the State of São Paulo, Brazil, established a program for a detailed genetic investigation of the species *Coffea arabica*, connected with an extensive breeding project.* At present but little is known about the origin and genetic constitution of our coffee varieties. The first problem that faced the writer was the working out of a simple and efficient technique for selfing and crossing coffee flowers on a large scale.

Flower Morphology

Figure 14*B* illustrates a typical coffee flower shortly after opening of the bud.

*This work is being carried out in cooperation with J. E. T. Mendes of the Agronomy Department of this Institute.

COFFEE FLOWERS

Figure 14

The jasmine-like flowers of coffee appear in the spring, which in the southern hemisphere occurs in September and October. During about a week all the plants in a region are covered with flowers. This main flowering period is preceded and followed by secondary bursts of bloom. *A* shows the flowering habit of the plant. *B* shows front and side views of flowers about natural size and *C* shows emasculated flowers in which the pistils have matured and are ready to be pollinated.

SECTION THROUGH FLOWER
Figure 15

Microscope section through an unopened flower showing the relative position of stigma and anthers. This demonstrates that the anthers are in close contact with the stigma lobe and that cross pollination is possible before the flower opens.

Several authors have described its morphology; the following summarized description has been partly taken from Cheney[1]:

Flowers subsessile or shortly pedicellate, 2 to 9, generally 3 to 5 together in very short axillary bracteolate clusters; calyx rudimentary, 5-denticulate; corolla white, lobes 5 to 6, oval, obtuse or acute equalling or generally exceeding the corolla tube, spreading. Anthers rather shorter than the corolla-lobes, wholly excerted, fixed rather below the middle to the filaments, which are about half as long as the anthers. Disc glabrous, style about equalling the unexpanded flower, bifid; lobes linear, narrower toward the tip, with the receptive stigmatic surface on their inside.

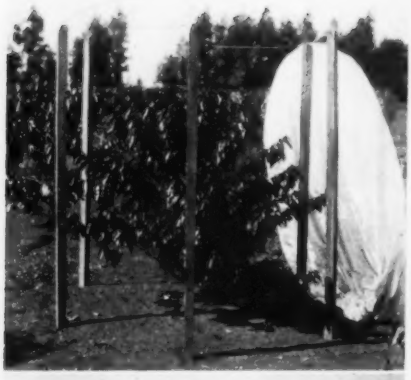
Observations on Flower Biology

Under the climatic conditions of the State of São Paulo, there is generally one principal flowering period shortly after the first rains in September or October. This takes place during two or three days, and during this period all the plantations in a whole region are covered with many millions of the white jasmin-like coffee flowers Figure 14*A*). This main period of flowering is generally preceded and also followed by several less intensive flowering periods which occur sometimes from June on until December.

No accurate observations have been published as yet on the biology of the flowers of varieties of *C. arabica*.* Cramer and van der Wolk[2], Zimmermann[5], and Taschdjian[4] have furnished some data on this subject, but they do not agree with respect to the intensity with which each of the many factors operate in pollination. Summarizing, the following may be stated regarding this subject: the flower-bud generally opens under normal conditions, on sunny days, early in the morning, and pollen shedding starts shortly afterwards; the stigma is receptive at the opening of the bud. The flower-morphology permits natural self-pollination. All commercial arabica varieties are self-fertile. Coffee flowers are intensively visited by insects, as common bees, small wild bees, wasps, and butterflies. Pollen is produced in a relatively small quantity, it is not sticky, and therefore probably may be carried by the wind; it may also fall by gravity to flowers on other branches at a lower level.

On cloudy days, however, the buds remain closed, even if they are already well developed. When fully developed buds fail to open because of a lack of sunshine, the maturation processes in the anther-sacs go on normally, independent of external influences. As a consequence of this the pollen is very often shed inside the closed flower-bud. The writer is unable to agree, therefore, with Taschdjian's statement that self-pollination is prevented due to the relative position of stigma and anthers; the cross-section shown in Figure 15 illustrates clearly that the anthers are in close contact with the stigma lobes in that stage of development of the bud, and are not separated as Taschdjian states. Besides a varying degree of self-pollination, the transfer of pollen is affected mainly by insects; and probably to a small degree also by the wind and by gravity. Two days after the opening of the flower-bud, the corolla begins to wither, and a few days later, if fertilization has occurred,

*Detailed observations are being made at present by the author and his associates, which will be published soon in another paper.



AUTOMATIC SELF FERTILIZATION OF COFFEE

Figure 16

Where large quantities of self fertilized seed is desired a cloth cover is put over the entire plant and left on for about a week during the flowering season.

PROTECTION OF FLOWERS FROM FOREIGN POLLEN

Figure 17

Cloth bags are placed over the branches a day or so before flowering begins. The flowers must be emasculated if they are to be used for hybridization.

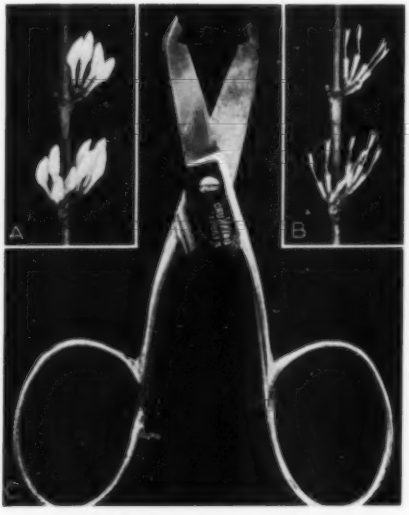
all flower parts, except the ovary, drop off. If pollination does not occur, the style and stigma generally remain turgid for many days.

Hybridization

Cramer and van der Wolk furnished in their article on coffee improvement the only available source of information about pollination work carried out by them in Java.* To insure self-fertilization they covered the flower-buds with small impermeable paper bags. For crossing purposes they emasculated the flower-buds two or three days before the opening, protecting them afterwards with paper bags; at the same time they labeled on the same plant a few other flower-buds at the same stage of development. When these opened, they pollinated the stigmas of the emasculated flowers by pouring the pollen from other anthers (from open flowers of the male parent) on them. Emasculation was carried out with a knife or common scissors, detaching the whole corolla with the inserted anthers. The pollinated flowers were kept protected in paper bags for about a week. Taschdjian[4] states that anthers from several flowers are necessary to pollinate with reasonable success one emasculated flower; the writer, however, succeeded in pollinating as many as five, and even eight emasculated flowers with the anthers of only one flower of the male parent.

Technique of selfing. In order to insure self-fertilization it is, of course, necessary to protect the flowers mainly against insects and also against the contamination by foreign pollen occasionally carried by the wind. Common paper bags, about 12 × 18 inches and elongated cloth bags have been used to cover individual branches about a day before the flower-buds opened. The cloth bags are tied at one end to the base of the branch and

*H. R. Lambers has also published on artificial crosses in coffee. (*Bergcultures* 7-1933.) Unfortunately this paper is not available to the author.



EMASCULATION OF FLOWERS
Figure 18

The stamens are removed by the use of a pair of scissors with notched blades which cut through the corolla but not into the pistil. *A* and *B* are two views of a group of flowers before and after emasculation by this method. *C* shows the scissors with which the operation is performed. When the scissors are closed the notches leave a small gap through which the style extends. A stop between the handles prevents the blades closing too far.

the other end is fixed on bamboo sticks as seen in Figure 17. Before covering up the branches it is, of course, first necessary to eliminate all small fruits generally present, which originated from a preceding flowering. The cloth bags have internal wire-rings in order to keep them open. About six days after flowering the bags can be taken off. At this time all the corollas that are dried up, and also most of the styles and stigmas that have turned black and shriveled are an indication that fertilization has occurred. The styles and stigmas which at that time are still white and turgid, must be removed with the help of small scissors. Should many turgid styles be left by this time, it is best to keep the branch covered for a few days more. Each branch with self-fertilized ovaries is then labeled. A fruit setting frequently as high as 80 per cent is obtained by this method.

If a large amount of self-fertilized seed from a limited number of individuals is needed, these may be covered up entirely by large cloth covers as is shown in Figure 16. These cloth covers are kept over the coffee shrubs for a period of about a week. From three- to four-year-old coffee shrubs as are shown in the preceding figures, as much as two pounds of clean seed was obtained last year by this method, each pound containing about 8,000 seeds.

Technique of crossing. In order to carry out a large number of crosses Cramer and van der Wolk's method has been somewhat simplified by the writer. The method used was as follows: flower-buds that would have normally opened in about two days, were emasculated, an operation which is performed with ease and rapidity with a pair of scissors especially adapted for this kind of work (Figure 18*C*). As can be seen in this figure, a small nick was made in each blade of the scissors; a piece of wire attached to one of the handles prevents the blades from closing entirely, and thus the aperture formed by the meeting of the two nicked blades is never entirely closed. In order to emasculate a flower-bud, the scissors are applied with the notches in the blades approximately at the middle of the corolla-tube; by closing the scissors, one only cuts the corolla-tube, leaving the style untouched, because of the construction of the scissors. With a light upward movement one pulls the whole corolla off and together with it the inserted stamens without touching the extremely sensitive female organs at all (Figures 18*A-B*).

After emasculating at least ten, (sometimes as many as fifty flower-buds on one branch), and after having eliminated with great care all the small fruits produced by earlier flowering, the whole branch is covered with a paper bag or an elongated cloth bag such as is used for selfing. Afterwards the branch is labeled with a red label bearing the date of emasculation; red labels are to be preferred, because they are easily found

later on, when the bags have been taken off. At the same time a few branches of the male parent shrub with flower-buds of about the same size as those used for emasculation, are covered with bags. This procedure is necessary to prevent contamination from foreign pollen (carried by insects and the wind) of the flowers that are expected to furnish pure pollen for the crosses. Two or three days afterwards, the stigmas of the emasculated flowers are examined; by that time the lobes are generally well expanded and receptive. Then the open flowers from the protected branches of the male parent shrub are collected by means of sterilized forceps, and carried to the female parent in small closed glass containers.

Pollination is effected by touching the inner sides of the stigma-lobes with the pollen-shedding anthers of the collected flowers. This operation is also performed with sterilized forceps. If there are many open flowers on branches above those being pollinated, it is necessary to protect the flowers below with a large piece of card-board during the operation to prevent the contamination of the emasculated flowers. Extremely windy days are to be avoided for artificial pollination work. After pollination, the branch is again covered up with the bag, and the male parent shrub number is noted on the label. After about a week, the bags are taken off, and any white and turgid styles still left at this time are eliminated.

Special boxes were used to carry the material needed in this pollination work, and a card system was developed to check every cross. On it was entered such information as the number of flowers pollinated on each branch, the number of the male parent shrub, date of pollination, etc.

After finishing the pollination work, it is necessary to maintain a careful watch of all labeled branches in order to eliminate the young flower-buds that generally arise on them afterwards.

The coffee hybridization work was carried out last year on a rather extensive scale on the experimental farms of this institute. In addition to facilitating artificial inbreeding, the simplified emasculation process mentioned above enabled the writer and his associates to make over two hundred different crosses. A total of 6,215 flowers were artificially pollinated and a total of 3,118 fruits were harvested. Thus a little over 50 per cent of the artificially pollinated flowers set fruit. These fruits furnished about 6,000 hybrid seeds. The aim of this hybridization program is not only to study the genetic constitution of the many varieties and other variations of *Coffea arabica*, but also to breed new hybrid varieties combining valuable economic characters at present distributed among several cultivated forms.

Summary

In the State of São Paulo, Brazil, there is generally one chief flowering period shortly after the first rains in September or October; it is preceded and followed by less intensive flowerings. Besides a varying degree of self-pollination, the transfer of pollen is caused mainly by insects and probably to a small degree also by the wind and the gravity. To insure self-fertilization, whole branches with flower buds are covered with paper or cloth bags shortly before opening; also whole shrubs may be covered up with large cloth covers. A detailed description is given on the technique of crossing; a new method of emasculation with the aid of a modified pair of scissors is described. This method makes possible easy and rapid emasculation of the flowers. Over 6,000 flowers were artificially pollinated in 1933 in this institute, with over fifty per cent success.

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INHERITANCE OF WRYTAIL IN JERSEY CATTLE

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WRYTAIL is the term applied when the base of the tail is set at an angle to the backbone. This abnormality has been observed in some breeds of cattle, horses, hogs, and poultry. Most of the instances have been attributed to accidents. A search of the literature has revealed no suggestions that this character might be inherited. The authors have noted many examples of this character in the Jersey breed, but the instances represented a small percentage of the total number of cattle which they have observed over a period of twenty years, and the affected animals were widely scattered with no apparent close relationship. When several wrytailed calves, all sired by the same bull, appeared in one herd of registered Jersey cattle the question of whether this is a heritable defect presented itself. It is interesting to note that the base of the tail was set to the left on all the affected animals reported in this study.

Should this character be proved hereditary, not only would it be an addition to the limited number of known heritable characters in cattle, but breeding methods for its elimination or control would be of value to breeders of purebred dairy cattle.

Observations of Breeders

Correspondence with breeders who have observed this character has indicated that animals may appear to be affected when young and yet may not show the defect later in life. The number of breeders making this statement would lend some credence to the observation, yet the experience of the authors has been that while there was some difficulty in positively identifying cases of wrytail in new born calves, in no instance has a case of wrytail been observed to become normal.

In order to check on the previous observations of the authors and to get some idea of the prevalence of this defect in various breeds of dairy cattle, letters were sent to leading dairy cattle judges, recognized breeders, and representatives of the different national breed associations. All of the replies received reported that this character was observed occasionally, even among some of the best cattle. The correspondents were quite unanimous in assuming that the cases observed had been due to injury, both because of the rarity of the defect and because the cases were so widely distributed.

The authors were positive that many wrytailed animals had been observed in the Jersey breed in past years but could not remember having seen the defect in the Holstein, Ayrshire, or Brown Swiss breeds. They were less certain as to whether they had observed this character in the Guernsey breed. Our correspondents were asked to state in which of the breeds they could positively remember having seen the wrytail character. Practically all of them reported having seen an occasional case in the Jersey breed but the reports on other breeds were not so unanimous. The following extracts from some of the letters are typical of the answers:

> I do know that we get quite a number of letters on this difficulty with Jerseys.
>
> . . . it has been my observation there are quite a few occurrences of wrytails in the

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Jersey breed. . . . However, they are not so common.

One occasionally sees a cow with a setting on one side but this is not peculiar to any family (Island of Jersey).

Most of the cases I have seen I have considered that they were due to accidents. . . . I have seen more wrytails in Jersey cattle, but I believe I have seen it in Guernseys as well.

I am under the impression that I have observed similar cases within the Jersey breed and I believe that I have seen one or two Guernseys with this defect. However, I am not sure about this. I am sure that I have never noticed this defect in Holstein, Ayrshire, or Brown Swiss herds.

I have seen this characteristic quite often but they were all isolated cases. (Guernsey breed.)

I would say that I have not noted very many cases of wrytailed animals within the Ayrshire breed. I do recall having seen a few of them, but there was apparently no relationship between them.

I distinctly remember observing wrytail in Jerseys, Holsteins, and Guernseys.

I do not recall that I have ever observed cases of wrytailed Holsteins.

I can only recall one case that I have noticed and that is a bull calf born in our own herd something over a year ago. . . . We laid it to injury at birth (Holsteins).

It must be considered that these answers were given from memory covering many years in most cases. It would appear that the wrytail character has been observed by most of these leading men in the dairy industry. One might gather that the character is present in the Guernsey breed, but possibly not to such an extent as in the Jersey breed. Conflicting statements in regard to the Holstein, Ayrshire, and Brown Swiss breeds would indicate that wrytail may not occur in these breeds as often as in Jerseys and Guernseys, and possibly not at all in some of these breeds.

Although in each case reported in this paper the wrytail was set to the left of the spinal column, the writers are not in a position to state whether this condition is more prevalent than wrytails set to the right, or whether the direction of the set of the tails is governed by heredity.

Wrytails in Progeny of Sire *B*

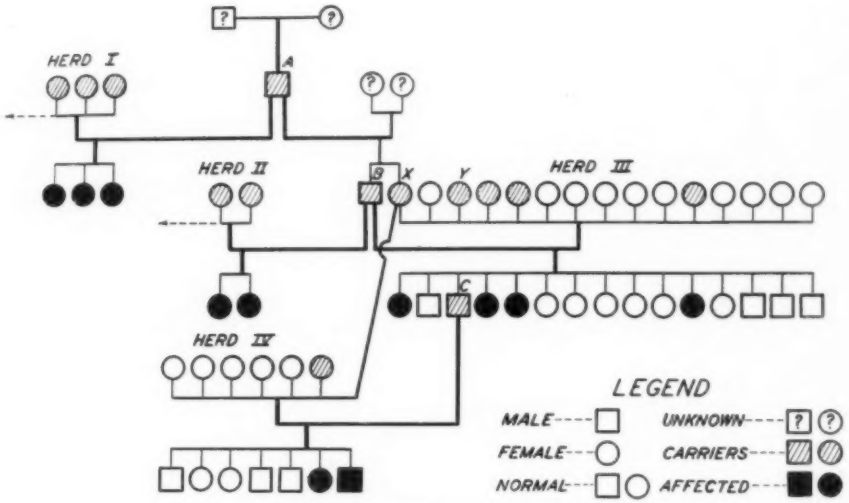
The problem first presented itself as the result of using sire *B* in herd III (see Figure 20). This bull was normal; that is, his tail was straight. Of fifteen offspring, four were wrytailed, although their dams were normal. The previous owner of this bull reported that over a period of several years quite a number of wrytailed calves had been born in his herd but was inclined to think that many of these were normal when mature. Two mature cows sired by this bull and still in the herd were positively identified as wrytailed, proving that the bull had also sired wrytailed offspring in herd II. The former owner reported that the bull used previous to sire *B* had also sired some wrytailed calves.

Investigation showed that sire *A*, the sire of bull *B*, had three mature living daughters that had wrytail and it was known that the dams of these three cows were all normal. Personal reports and pictures indicate that not

THE WRYTAIL CHARACTER

Figure 19

The tendency for the base of the tail to be set at an angle to the vertebral column appears to be an inherited characteristic. It seems to be most common in Jersey cattle, but has been noted also in several other breeds. In all cases observed the tail has been set to the left. The character is undoubtedly inherited (see Figure 20).



INHERITANCE OF WRYTAIL
Figure 20

Since wrytail affects both sexes and is transmitted through normal appearing individuals, it is probable that the character is inherited as a simple mendelian recessive.

only was sire *A* normal, but so were his sire and dam.

These facts indicate that sire *A*, although normal in appearance, carried the factor for wrytail. Which parent contributed this factor is not known. Sire *B* also carried the factor but it is not known whether or not his dam was normal. Although sire *B* was normal he could have obtained the factor for wrytail from his sire, sire *A*, known to be a carrier.

Not only were four out of fifteen offspring from sire *B* wrytailed, but the most exaggerated case was the result of mating him with his own normal half sister (*X*), both being sired by sire *A*. In this instance the tail-head was set almost at right angles to the spinal column.

When sire *B* was mated with the normal cow *Y* the result was sire *C*. This bull was normal and out of a normal dam but when used in herd IV produced two wrytailed and five normal calves. It is interesting to note that one of the wrytailed calves was from cow *X*, mentioned above, which had been sold from herd III. This cow was by sire *A*, thus being a paternal half sister to sire *B*, and was proved to be a carrier of the factor when a wrytailed calf was produced by mating her with sire *B*.

The results show that in three consecutive generations of bulls (sires *A*, *B*, and *C*) all appeared to be normal but apparently each individul was heterozygous for wrytail. In herds I and II the matings illustrated in Figure 20 indicate the genotype of sires *A* and *B*, respectively, which are of interest in showing how the factor for wrytail may be carried from generation to generation by apparently normal animals. The data on herds I and II are not of much value in attempting to analyze the mode of inheritance of wrytail.

Although sire *C* is a son of sire *B*, both are heterozygous for the character, and segregation of homozygous individuals (wrytailed) took place among offspring of each. The offspring of these two sires in herds III and IV, therefore, should be considered F_2 individuals and in studying the mode of inheritance the data from the two herds may be combined, since both bulls are known to be heterozy-

gous. The segregation in the two herds combined showed six wrytailed offspring and twenty of normal appearance.

Mode of Inheritance

The data presented lend themselves to a monofactorial hypothesis. The factor for wrytail seems to be recessive to normal setting. The offspring in herds III and IV closely approached the ratio of 1 wrytailed to 3 normal, as would be expected by this hypothesis. The fact that the factor for wrytail apparently is widely scattered through the Jersey breed, although cropping out only occasionally, would further indicate that it is a recessive character. Apparently the wrytailed animals result from parents both of which carry the factor whether they are normal (heterozygous) or wrytailed (homozygous). Positive proof of this hypothesis could be obtained by crossing a wrytailed bull back on his own daughters which should result in 50 per cent of the F_2 generation from normal (heterozygous) daughters being wrytailed, and all of the F_2 daughters from wrytailed (homozygous) daughters being affected.

Representing the dominant factor (normal) by *N* and its recessive allelomorph (wrytail) by *n*, the phenotypically normal individuals would genotypically be either *NN* or *Nn* while the wrytailed individuals would be *nn*.

Practical Applications

If wrytail is a recessive character widely scattered through the Jersey breed and possibly other breeds of dairy cattle, then it will be difficult to eliminate, as are all recessive characters. Breeders should not use wrytailed animals of either sex, but it is evident that the use of a wrytailed bull is much more serious because of his ability to beget many more offspring than an individual cow. Such a bull will necessarily transmit to all his calves a single "dose" of this factor, even though no wrytailed individuals are found among his offspring. When a second bull, normal in appearance but heterozygous for wrytail is used, he is too often charged with the sole responsibility for the affected animals that result. Two normal appearing bulls, heterozygous for wrytail, could be responsible for this character cropping out in a herd even though they were used several generations apart. A herd sire might be tested for absence of this factor by breeding him to a number of wrytailed cows. If no wrytailed offspring resulted the owner would be safe in considering the bull free from this factor, provided enough matings were made. This is hardly practical, however, and the best that can be done probably is to discard wrytailed animals of either sex from the herd. When it becomes generally known among breeders of purebred dairy cattle that wrytail is a heritable character, affected animals will be discriminated against and the sale price of such animals will be reduced. Affected animals should be properly penalized in the show ring according to the following rule published by the American Jersey Cattle Club: "Animals having hereditary or functional defects will be disqualified by the judge. For example—total blindness, bull having only one testicle, etc."

Summary and Conclusions

1. Four out of fifteen calves in a single herd sired by one Jersey bull being wrytailed led to study of this character.
2. Three consecutive generations of normal sires were proved to be carriers of the factor for this character.
3. This character is definitely heritable and appears to be monofactorial with wrytail recessive to normal.
4. Apparently the character is widely disseminated through the Jersey breed and possibly other breeds of dairy cattle.
5. Elimination of the character entirely will be difficult but it should be discriminated against in purebred herds.

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